EFFECTS OF HABITAT USE BY NATIVE WILDLIFE ON CATTLE FEVER TICK POPULATION DYNAMICS IN SEMI-ARID RANGELANDS: SIMULATION OF POTENTIAL CONTROL STRATEGIES

A Dissertation

by

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ABSTRACT

I developed a spatially-explicit, individual-based simulation model, parameterized to represent ecological conditions typical of the south Texas, to examine effects of shifts in habitat use by white-tailed deer (WTD) on the population dynamics of *Rhipicephalus (Boophilus) anulatus* and *R (B) microplus*, collectively known as cattle-fever ticks (CFT), and its influence on potential control strategies.

At the landscape level, simulated changes in WTD habitat preferences did not seem to have an effect on CFT densities when cattle were present in the system; however, habitat-level differences were observed, especially within mixed-brush habitats. When cattle were present, the role of WTD habitat preferences went largely unnoticed, especially in those habitats more preferred by cattle, suggesting that cattle dominate the system and that there is a spatial scale component influencing the effect of WHT habitat preferences.

Similarly, when examining the effect of pasture vacation as a CFT eradication strategy, landscape-level differences in CFT densities were not evident across WTD habitat preferences, while differences were observed at the habitat level, especially within mixed brush, suggesting that there is an interaction between habitat preference and habitat suitability that influences the response of CFT to different host/eradication scenarios at the habitat level.

Densities of CFT in grass, the poor habitat for CFT but preferred habitat by cattle, did not seem as influenced by WTD habitat preferences as by the host/eradication scenario; densities in mixed-

brush, the habitat least preferred by cattle and fair for CFT, seemed to be influenced by changes in habitat preference; and densities in mesquite, the best habitat for CFT, constantly supported high densities regardless of host or eradication scenario.

Despite consistently supporting the lowest densities of CFT, mixed-brush was the habitat type where the largest differences among habitat preferences were observed, regardless of host/eradication scenario, suggesting that it plays an important role in sustaining CFT populations, with implications for eradication strategies

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Contributors

This work was supervised by a dissertation committee consisting of Professors William E. Grant and Miguel Mora of the Department of Wildlife and Fisheries Sciences, Dr. Selma Glasscock of the Welder Wildlife Foundation, and Dr. Merwin Kothmann, Professor of the Department of Ecosystem Science and Management. All the work conducted for the dissertation was completed by the student independently.

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TABLE OF CONTENTS

Page

LIST OF TABLES

Page

LIST OF FIGURES

Page

1 INTRODUCTION

Ticks, considered one of the most important blood-sucking arthropods worldwide (Guglielmone et al. 2014), were the first arthropods to be clearly established as vectors of infectious disease, after the discovery by Smith and Kilbourne in 1893 of the role of *Rhipicephalus (Boophilus) annulatus* as the vector of *Babesia bigemina* (Mullen 2019).

Rhipicephalus ticks have been identified as vectors of several diseases, including babesiosis, anaplasmosis, and borreliosis (Giles et al. 2014, Hailemariam et al. 2017), with important economic and health implications (Food and Agriculture Organization [FAO] 1984, de Castro 1997, FAO 2004) both for animals (Raoult and Roux 1997, Duttmann et al. 2016, Melhorn 2016) and humans. The risk of tick-borne zoonotic diseases is of great concern for public health authorities because of their increasing geographic range and the potential emergence of pathogens (Vorou et al. 2007, Jones et al. 2008).

There are five species of hard ticks (Ixodiade) that mainly infest livestock: *R (B) annulatus*, *R (B) decoloratus*, *R (B) geigyi*, *R (B) kohlsi*, and *R (B) microplus*; the taxonomic status of these five species has undergone several changes since first described (Murrell and Barker 2003). Originally included in separate genera (*Ixodes*, *Rhipicephalus*, and *Haemaphysalis*), they were later grouped under the genus *Boophilus* and in 2003, based on morphological and molecular studies, Murrell and Barker (2003) proposed assigning these five species to the subgenus *Boophilus* within the genus *Rhipicephalus*.

Boophilus sp ticks, which occur worldwide in most tropical and subtropical regions (Nicholson et al. 2019), are one-host parasites of ungulates, completing their life cycle on a single host. The larval, free-living stage, constitutes up to 90% of the total life cycle of *Boophilus* sp ticks (Needham and Teel 1991), and therefore is exposed longer to environmental conditions (Leal et al. 2018). Host-seeking larvae attach to a host, then they feed, molt into nymphs, and then feed again to molt into adults, before dropping from their single host, laying eggs, and dying.

Initially introduced to the Americas by European colonists, *R (B) anulatus*, native to the Mediterranean region, and *R (B) microplus*, native to tropical and sub-tropical regions of southern Asia, have widely dispersed throughout subtropical and tropical regions worldwide (George 2000, Bram et al. 2002). Several studies have confirmed their colonization potential and invasive characteristics through displacement of indigenous ticks of the same genus (De Clercq et al. 2012), causing significant damage to livestock production across their range (Davey et al. 1994, Frisch 1999).

R (B) anulatus and *R (B) microplus*, collectively known as cattle-fever ticks (CFT), are vectors of the protozoal parasites *B. bigemina* and *B. bovis* that cause bovine babesiosis (also known as cattle fever). This disease, which hit the cattle industry in the United States until ticks were eradicated in 1942 (Assadian and Stanek 2002), inhibits growth and production, and eventually leads to death in susceptible untreated animals (Rodríguez-Vivas et al. 2018). These ticks and pathogens are still prevalent in Mexico, adjacent to the Texas border. Thus far, the Cattle Fever Tick Eradication Program (CFTEP) has prevented re-infestations of CFT into the United States, except within and near the permanent CFT quarantine zone (quarantine zone), a permanent buffer zone along the

international border, extending approximately 800 kilometers along the Rio Grande (Figure 1.1; Bram et al. 2002).

Two traditional methods of CFT elimination involve the use of acaricides and the implementation of pasture vacation (Graham and Hourrigan 1977). The first method requires systematic dipping of all cattle with a topical acaricide, unless no CFT are found after inspection of animals and premises. The second method requires removing all domestic hosts from infested pastures for a period long enough to guarantee that all free-living larvae have died from desiccation or starvation (Texas Animal Health Commission [TAHC] 2017). Vaccination of domestic livestock is an alternative to the chemical treatment (Hernandez 1998); however, the vaccine effect is not immediate and its action takes place over long periods of time. Vaccination and dipping have to occur simultaneously (Ruvalcaba-Fernandez 2009), and the risk of a spread and establishment of CFT beyond the quarantine zone remains a valid concern for the cattle industry, with costly consequences (US Department of Agriculture [USDA] Animal and Plant Health Inspection Service [APHIS] 2010).

Within the quarantine zone, all livestock and live or hunted wildlife that are capable of hosting CFT, are subject to movement restrictions, inspections, and treatment, as prescribed by TAHC CFT regulations (TAHC 2019a). The CFTEP protects cattle in portions of eight South-Texas counties (Cameron, Live Oak, Kinney, Maverick, Starr, Webb, Willacy and Zapata) and 13 other southern states from the re-introduction of bovine babesiosis, by the two CFT species in Mexico (Graham and Hourrigan 1977). In recent years, however, and despite eradication and control strategies, expansion of CFT infestations have resulted in quarantines outside of the quarantine

zone, in a region known as the “free area” (Texas A&M AgriLife Extension 2019), re-emerging as a serious threat to the livestock industry.

Several factors have been listed as responsible for the dramatic increase in the number of CFT infestations within the quarantine zone and their expansion into the free area. These factors include close proximity to infestations of both CFT species in Mexico, the large numbers of cattle being imported from Mexico and pastured in the free area, and the increase in density of white-tailed deer (WTD; *Odoicoleus virginianus*) in Texas (Pound et al. 2010). Despite eradication and control strategies, a zone covering almost 404,686 hectares (ha) was quarantined in South Texas in 2009, more than the previous four decades, due to CFT outbreaks outside the quarantine zone (USDA APHIS 2013). As of 2019, an area covering approximately 301,315 ha is under various types of CFT quarantine outside of the quarantine zone (TAHC 2019b).

Figure 1.1. Historic extension of the infestation[1] of the Cattle Fever Ticks (CFT) *Rhipicephalus (Boophilus) microplus* and *R (B) annulatus* in the United States (blue area; top panel) and the location of the current quarantine line (solid red line; top and bottom panels), the permanent quarantine zone (in yellow; bottom panel), and the temporary preventative quarantine area (in blue; bottom panel), with location of current infestations[2] of CFT along the Texas-Mexico border.

[1.] The land in blue was infested before the CFT Eradication Program began in 1906. Adapted from the US Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS; 2010). Public domain image available on the internet and included in accordance with Title 17 United States Code Section 107.

[2.] Infestations as of 2017 within the permanent quarantine zone (red stars) and the free area (green stars) are shown. Adapted from USDA APHIS 2018b. Public domain image available on the internet and included in accordance with Title 17 United States Code Section 107

Emergence of infectious diseases often results from interactions among wildlife species, domestic animals, and zoonotic pathogens. Security is threatened by wildlife tick hosts that share rangeland with cattle and present challenges to cattle-centered regulatory approaches (Pérez de León et al. 2012). An understanding of the complex ecological relationships among species, and between species and their environment that support disease transmission, allows for quantification of risk to livestock and subsequent implementation of preventative measures to reduce this risk. Thus, understanding the role of wildlife populations on vector transmission and its effects on livestock health has become increasingly important due, in part, to its implications for human health and economy (Uilenberg 2006, Tay et al. 2014).

The WTD, native to North America, is a confirmed host for CFT, posing risks to their re-establishment in the United States (Pound et al. 2010). Serologic and molecular evidence suggest that WTD carry bovine babesiosis in southern Texas and northern Mexico (Holman et al. 2011), highlighting the importance of understanding risk factors associated with the transmission and maintenance of vectors and pathogens.

Field studies examining the role of alternative hosts in sustaining and spreading CFT are not permitted due to regulatory restrictions (Pound et al. 2010); however, confirmed presence of *B. bigemina* and *B. bovis* in exotic ungulates in northern Mexico (Cárdenas-Canales et al. 2011), and possible presence of this pathogen on exotic ungulates in Texas (Olafson et al. 2018), illustrate the additional threat that non-native wildlife pose to the CFTEP and to cattle enterprises.

Alternative management strategies for tick suppression have been developed and applied. Game fencing has been employed to prevent crossing of infested hosts onto Texas from Mexico (Gortazar et al. 2015), bait stations have been utilized to treat WTD with ingested or topical acaricides (Pound et al. 1996, 2000), vaccination of WTD has been explored (Estrada-Peña A 2014), and prescribed fires as a control strategy in chaparral and oak woodland habitats have been studied, with limited results (Padgett et al. 2009, Gilliam et al. 2018).

The efficacy of the CFT control and eradication programs is challenged by several factors, including limitations in the extent of the application and treatment of wild ungulates (Currie 2013), evolution of resistance to organophosphate and pyrethroid acaricides (Abbas et al. 2014), the presence in South Texas of dense populations of WTD and exotic ungulate species that are alternate hosts for CFT (Lohmeyer et al. 2018, USDA APHIS 2018b), and changing plant communities that provide an abundance of habitats favorable to the survival of CFT (Pérez de León et al. 2012). These challenges emphasize the need for alternative treatment strategies that can be implemented on cattle (Ghosh et al. 2007, Pound et al. 2010). Perhaps of equal importance is the need to have alternative treatment methods and strategies available for eradication of infestations of CFT feeding on WTD and exotic ungulate species.

CFT control programs in Australia and Mexico have met similar difficulties (Angus 1996, George et al. 2002, Cutullé et al. 2009). Besides the need for practical and efficacious tick control technology, there is a need of a better understanding of the major risk factors that lead to the re-introduction of ticks. Predictive risk assessment models of the reoccurring CFT infestations within and near the quarantine zone are a valuable tool for broadening our understanding of these complex

systems and improving eradication strategies. New concepts for tick suppression will aid in the continued effort to prevent CFT spread, which, if left unchecked, will increase economic and animal health burdens for producers and landowners.

Pérez de León et al. (2012) stressed the importance of habitat use and home range management of wild and exotic hosts to be integrated into future efforts aimed at eliminating CFT outbreaks. Previous studies on the population dynamics of CFT have used simulation models to explore the climate-tick-host-landscape interaction (see Wang et al. 2017 for a complete review). Few studies, however, have considered host habitat preferences within the context of this interaction (Wang et al. 2016), and none, to my knowledge, have explored the effects of changes in host habitat preferences, despite the recognized importance of host habitat usage in predicting the transmission of tick-borne pathogens (Estrada-Peña et al. 2008, Wang et al. 2012).

The main objective of this study is to explore the role of native ungulates in sustaining populations of vectors of disease to domestic livestock in semi-arid landscapes. More specifically, I used a spatially-explicit, individual-based model to (1) simulate the interactions among CFT, WTD, and cattle in South Texas, and to (2) explore the effects of WTD habitat preferences on the dynamics of CFT populations in regards to the efficacy of CFT eradication programs.

2 LITERATURE REVIEW

Several pathogens have the potential to infect populations of sympatric host species simultaneously and many wildlife species are reservoirs of pathogens of importance for domestic animal and human health. These multi-host situations have been documented for several diseases such as toxoplasmosis and feline immunodeficiency virus (Gauss et al. 2006, Bevins et al. 2012).

Wiethoelter et al. (2015) conducted an extensive search of the scientific literature on infectious diseases at interfaces between wildlife and livestock; their desktop review indicated an increase in publications on the ungulate-cattle and bird-poultry interactions, with zoonoses research composing the majority of scientific publications identified. At the wildlife-livestock interface, examples of these studies include bovine viral diarrhea in cattle and roe deer (*Capreolus capreolus*) in Spain (Rodríguez-Prieto et al. 2016); *Mycobacterium bovis* in cattle, wild boars (*Sus scrofa*), badgers (*Meles meles*), and red (*Cervus elaphus*), and roe deer in France (Réveillaud et al. 2018); and brucellosis in a broad range of livestock and wildlife in Europe (Garnett et al. 2002).

Global change augments instability in ecosystems and ecosystem services through disruptive processes that can drive the emergence or re-emergence of diseases (Epstein 1995, Githeko et al. 2000). Global change alters the population dynamics of ticks and the epidemiology of tick-borne diseases via shifts in ecological processes influencing tick biology and consequently the epidemiology of pathogens transmitted by ticks (Tabachnick 2010, Randolph 2010), making human and animal populations vulnerable to new and recurring tick infestations and tick-borne diseases (Pérez de León et al. 2012).

Bovine babesiosis, one of such tick-borne diseases, is considered the most economically important livestock disease worldwide (Gohil et al. 2013), requiring urgent attention (Wahlberg and Nyman 2001, Pérez de León et al. 2010, Rodríguez-Vivas et al. 2014). For example, it has been estimated that the livestock industry realizes annual savings of at least 3 billion dollars since the United States was declared free of both bovine babesiosis and CFT (Graham and Hourrigan 1977). Keeping cattle herds free of bovine babesiosis is an important economic and animal health issue (Pérez de León et al. 2012).

Tick feeding produces direct and indirect losses to livestock production (Uilenberg 1995). Direct losses, resulting from blood feeding and irritation, have negative impacts on reproduction and growth, as well as meat and milk production, and draft services (Betancur Hurtado and Giraldo-Ríos 2018). Indirect losses associated with tick-borne diseases include severe morbidity and, in extreme cases, mortality (Graf et al. 2004). Consequently, CFT have received much research attention in regions where they coincide with high cattle production, primarily in Australia and the Americas (Wang et al. 2017), since they have considerable economic, medical, and veterinary impacts (Homer et al. 2000, Bock et al. 2004).

There is concern about the disease, competitive, and genetic interactions among exotic, native and domestic ungulates and their long-term effects on rangelands and populations. Although cattle are the main host of CFT, they have also been documented on other wild, domestic, and exotic ungulates such as WTD (Cantú et al. 2007), sheep (*Ovis aries*; Mungall and Sheffield 1994), and Nilgai antelope (*Bocelaphus tragocamelus*; Sheffield et al. 1983). Despite having expanded their range of potential hosts, the degree to which CFT use alternate native and exotic wildlife hosts,

and the role that these hosts play as potential reservoirs of the disease agent, is still unclear (Pérez de León et al. 2010, Cárdenas-Canales et al. 2011, Chevillon et al. 2013, Olafson et al. 2018).

Although alternative hosts are of interest in understanding how CFT may be spread through the landscape, little is known about the habitat use and movement patterns of several exotic ungulates in Texas or on their native ranges (Foley et al. 2017). Movements of these free-ranging and largely unregulated hosts in South Texas are unlikely restricted by traditional cattle fencing, adding to the uncertainty in the efficacy of CFT control and eradication programs. To this end, the USDA published a final record decision to install tall game fencing (approximately 2.4 meters tall) along strategic portions of the permanent tick quarantine line in Zapata County, Texas (USDA APHIS 2018a).

WTD have experienced a remarkable expansion in Texas over the last 100 years, from less than 10,000 individuals in the 1900's, to a current statewide population numbering approximately four million (McDonald et al. 2004). The behavior, home and activity ranges, and movements of WTD have been widely investigated for management and conservation purposes (Felix et al. 2007, Hellickson et al. 2008, Webb et al. 2010). In many cases, however, several species of ungulates can be found on a given range, making difficult the understanding of ecosystem and landscape-level processes for the development and implementation of management plans (de la Fuente et al. 2015). Texas rangelands, in particular, support a wide variety of ungulate species including combinations of livestock, native wildlife, and exotics in large numbers (Armstrong and Harmel 1981, Traweek and Welch 1992, Armstrong and Young 2000). This complicates even further the assessment of intervention strategies, given that most pathogens of concern to livestock are able to infect several host species (Cantú-C et al. 2009, Cooper et al. 2010).

Based on the last survey conducted by the Texas Parks and Wildlife Department in 1994, there were 87 different species of exotics within the state, accounting for 118,265 individuals, most of which were found in the Edwards Plateau and South-Texas Plains Ecological Areas (Traweek 1995). Many Texas ranges have high stocking rates due to an extensive domestic cattle industry (Hanselka et al. 1991), large herds of native ungulates, especially WTD, and large numbers of exotics, of which axis deer (*Axis axis*) and Nilgai antelope were the most abundant, with 39,040 and 36,756 individuals, respectively, according the last official census (Traweek 1995).

Between 1940 and 2004, more than 335 emerging infectious disease events were reported in the scientific literature, the majority of which involved zoonoses with an epidemiologically important wildlife host (Jones et al. 2008). Cervid ungulates are important hosts for several zoonotic pathogens (Olsen 2010, Gnat et al. 2015), some of which are also transmitted to livestock, making these important diseases at the wildlife-livestock-human interface. WTD, in particular, are keystone hosts for both the blacklegged tick, *Ixodes scapularis*, and the lone star tick, *Amblyomma americanum*, which transmit disease agents causing Lyme disease, southern tick-associated rash illness, human ehrlichiosis, human babesiosis, and other diseases of humans throughout much of the United States (Palmer et al. 2017), increasing the human health need to control ticks feeding on WTD.

New and improved technologies developed to eradicate CFT on WTD can also be evaluated for potential in controlling these medically important ticks. Suppression of Ixodes and Amblyomma ticks on WTD has been a research focus in Lyme Disease and Ehrlichia endemic areas of

Northeastern United States (Carroll et al. 2002). Self-treatment devices for WTD that provide up to 90% control of these three-host ticks over periods between 3 – 5 years have been developed; however, not all animals can be treated, and whether these devices can be successful in the control against the one-host CFT in Texas rangelands is unknown (Fish and Childs 2009, Pérez de León et al. 2012, Stafford and Williams 2017). Other tactics including prescribed fire, fencing, and trap forage crops, are options being considered.

Livestock management practices can have a profound impact on wildlife population dynamics, and the key to successful, holistic management is to consider both domestic and wild animals as integrated parts of the ecosystem (Ortega and Bryant 2005). Cattle producers, medical and veterinary disease regulatory agencies, and citizens subject to tick-borne diseases or pestilence from ticks will benefit from this kind of approach; similarly, regulatory agencies will have more information to improve safe, efficient, and efficacious methods with which to sustain efforts to eradicate CFT.

In places where inter-specific interactions of wild and domestic animals increase the risk of transmission among species also increases, this is of particular concern to wild and human population health. Controlling ticks on wildlife has become critical to CFT eradication efforts because genetic data suggest WTD likely serve as a source for ticks on cattle (Busch et al. 2014). Further research is needed in order to determine the role both domestic animals and wildlife have on disease transmission and the effects of such diseases on native species (Martin et al. 2011, Gortazar et al. 2015).

Several causes have been proposed for the introduction and spread of ticks worldwide, including uncontrolled movements of domestic or wild animals, climate trends, and changes in abundance and distribution of tick hosts due, in part, to extensive land cover changes and the subsequent alteration and degradation of land resources as a result of human activities (Estrada-Peña and Salman 2013). Among the global issues, land degradation is especially important due to its impact on world food security and quality of the environment (Eswaran et al. 2001). Arid and semi-arid regions constitute approximately 25% of the contiguous United States and a significant fraction of the world's surface; they are home to at least 1 billion people whose livelihood is affected by the economic and social impacts associated with land degradation and the decline in the productive capacity of these areas (Eswaran et al. 2001).

Historically, the semi-arid rangeland ecosystems of North America and Africa were grazed by free-ranging herds of large, migratory herbivores that moved constantly, largely in response to changes in the quantity and quality of available vegetation (Frank and Groffman 1998). Grazing was intense for a short time at any particular site, but plants usually had time to recover between defoliation events (Frank and Groffman 1998). This periodic defoliation and regrowth of vegetation resulting from the activities of migratory herbivores was an integral part of ecosystem regulatory processes affecting not only the vegetation, but also the soil biota, the chemical and physical properties of the soil, and the hydrological processes (Teague et al. 2011).

Migratory grazers are considered drivers of primary production, with low levels of primary production at excessively low or high levels of herbivory and maximum productivity at intermediate levels of herbivory (McNaughton et al. 1989, Frank et al. 2002). Agricultural

intensification and the replacement of free-ranging wild herbivores with livestock or fenced-in animals has altered the periodic defoliation and regrowth cycles in semi-arid rangelands (Teague et al. 2011). It has also led to widespread overgrazing (Oesterheld et al. 1992), decrease in soil quality, pasture production, and biodiversity (Frank and Groffman 1998, Pulido et al. 2018), loss of ecosystem functional integrity (López et al. 2013), alteration of epidemiological patterns (Jones et al. 2013) and increase in disease risk (Stonenberg Holt 2018).

Host community composition and density, and landscape composition and habitat structure, as well as climate and human activities, influence tick ecology and tick-borne pathogen dynamics (Lindgren and Jaenson 2006, Randolph 2009, Diuk-Wasser et al. 2010). Understanding the regional and local factors influencing tick population dynamics requires an understanding of the feedback mechanisms between vegetation, wildlife, and livestock in a changing climate and environment (Miller et al. 2013, Wiethoelter et al. 2015), with implications for the application and efficacy of control strategies of pathogens and vectors of diseases and therefore, for the long-term productivity of rangelands.

Changes in the composition of landscapes can have effects on the distribution and persistence of a population (Turner and Gardner 1991), and the spatial mosaic of a landscape determines how a foraging animal responds to the distribution of resources. Studies of this relationship between processes (rates of animal movement and dispersal) and patterns (landscape structure and spatial configuration of habitat) are limited, and the underlying assumption of habitat perceived as a set of discrete entities, instead as of a continuum, has limited their application (Chetkiewicz et al. 2006). The importance of producing reliable correlative, pattern-based models when process-

driven models are unavailable has been stressed by Estrada-Peña et al. (2016) in the context of predicting the distribution of arthropod vectors as a response to climate change.

Our ability to assess immediate and future impacts of global change on these animal vectors and diseases needs to be enhanced (Pérez de León et al. 2012). Modelling has been increasingly advocated as a means to facilitate anticipation and improve prevention, preparedness, and the management of ticks and tick-borne diseases (Baylis and Githeko 2006, Garner et al. 2007, Munroe and Willis 2007, Woolhouse 2011). In a review of quantitative tick models reported in the scientific literature, Wang et al. (2017) reported a total of 101 articles for studies conducted over nearly 50 years. These studies varied widely in location (several regions across different continents), modelling approaches (analytical or simulation), and predictive focus (geographic distribution or population dynamics). Driving variables, temporal and spatial scales, and tick development and host-finding rates also varied widely among models, stressing the fact that no single modelling approach is best (Wang et al. 2017).

In the present study, I simulate the effects of changes in host habitat preference on the long-term (4 years) trends in CFT populations under conditions of climate, host community, and landscape composition typical of South Texas. I provide (a) an overview of the model, describing its general structure; (b) a summary of the long-term trends emerging from simulations, and (c) a discussion of these results within the context of current CFT eradication strategies.

3 STUDY AREA

I parameterized my model to represent environmental and landscape conditions typical of South Texas, United States. Based on the 30-year period (1981 – 2010) data from the National Oceanic and Atmospheric Administration (NOAA) National Weather Service (NWS), the mean rainfall in the Houston/Galveston area is approximately 124.5 centimeters per year, with a bi-modal distribution that peaks from May – June and September – October (NOAA NWS 2019). This distribution contributes to two periods following rainfall peaks in which plant growth is depressed: (1) a summer dry period and (2) a winter dry period with cooler temperatures (Box 1960, Finch et al. 2016).

Three habitat types, chosen on the basis of the dominant plant species or associations of species, were selected to be included in this study: mesquite-dominated community, mixed-brush-dominated community, and grass-dominated community (McMahan et al. 1984). Although plant communities are heterogeneous with regard to composition of species for a particular area, my characterization of habitat types on the basis of broad plant species associations was appropriate for the vegetation conditions commonly found on rangelands in South Texas, and adequately represented the landscape composition typically encountered by CFT and their ungulate hosts in this region.

4 METHODS

4.1 Model Description

The spatially-explicit, individual-based, stochastic model described in this section was developed to simulate the effects of climate, landscape, and habitat preferences of hosts on the population dynamics of CFT (Figure 4.1). Three habitat types, chosen on the basis of the dominant plant species or associations of species (*sensu* McMahan et al. 1984), were selected to be included in this study: mesquite-dominated community (mesquite), mixed-brush-dominated community (mixed-brush), and grass-dominated community (uncanopied grass).

This model, largely developed by modifying a previous model by Wang et al. (2016), represents the interaction among (1) climate variables known to affect CFT survival, development, and reproduction; (2) landscape attributes known to influence CFT survival, development, and reproduction, as well as use of space by hosts; (3) domestic and wild ungulates known to be hosts for CFT; and (4) habitat preferences of domestic and wild hosts potentially influencing CFT population dynamics (Figure 4.2 and Figure 4.3).

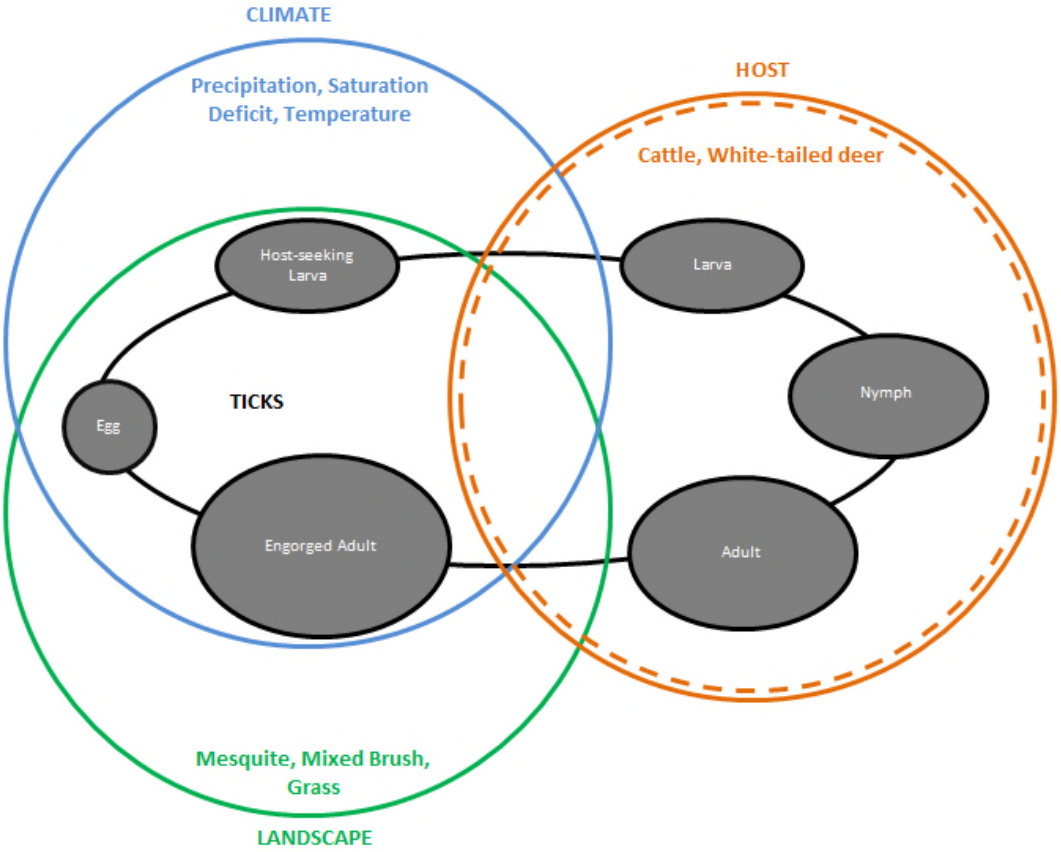

Figure 4.1. Conceptual model of the tick-host-landscape system, representing the spatial relationships and dynamic processes influencing the potential role of host habitat preferences in the maintenance of cattle-fever tick (CFT) populations.

Blue circle represents specific temperature, saturation deficit, and precipitation index conditions.

Black line represents the progression of CFT through their various off-host and on-host life stages (see Figure 4.3 for a detailed representation of the aspects of CFT life cycle included in the model).

Green circle represents a specific composition of habitat types within the landscape (see **Error! Reference source not found.** for a detailed representation of the hierarchical landscape).

Orange circle represents the host community. The dashed orange circle represents host-specific habitat preferences.

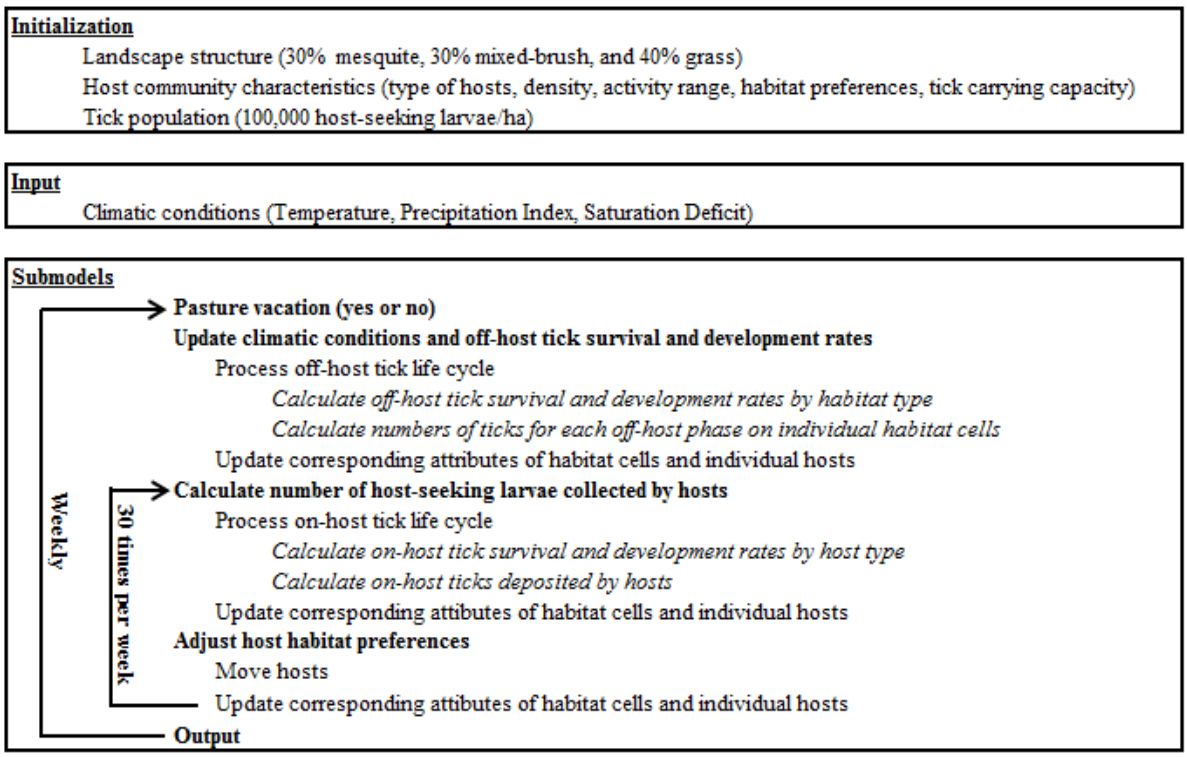

Figure 4.2. Overview of the sequence of events and processes involved in the execution of the model.

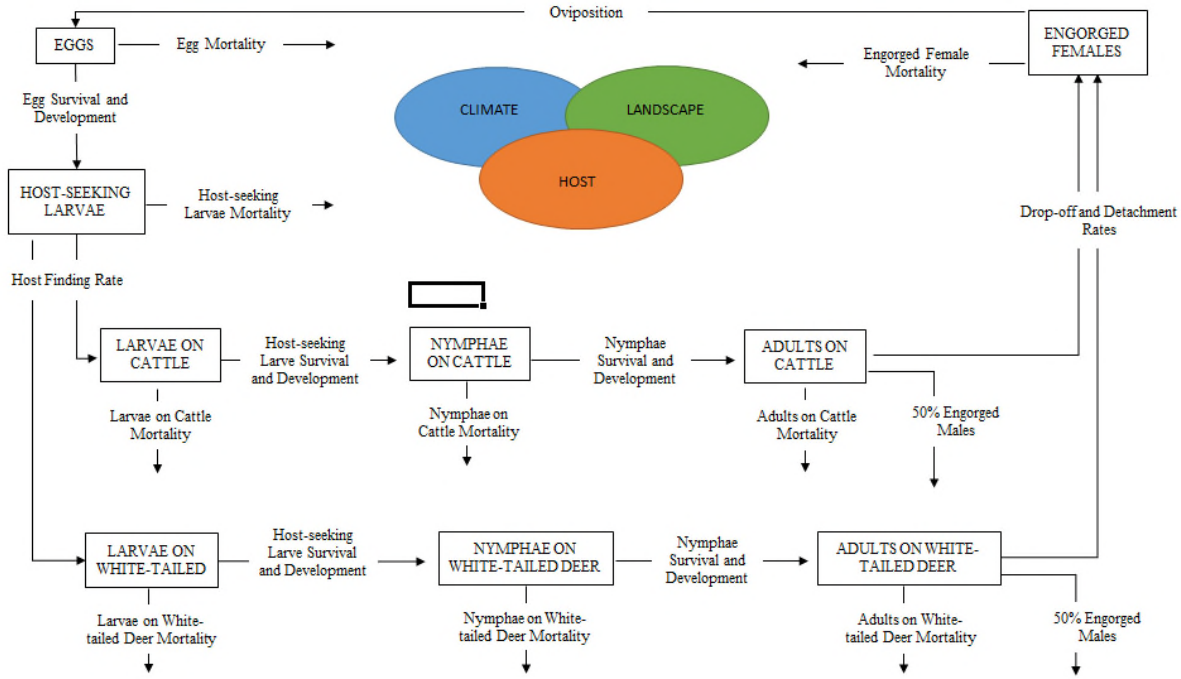

Figure 4.3. Representation of the various aspects of the cattle-fever tick life cycle included in the model.

The simulated landscape is composed of 900 individual cells, one-ha each, arranged as a torus, representative of a ranch facility in South Texas (Gleaton and Robisnon 2014). Attributes of individual cells include survival, development, and reproduction rates of off-host CFT life stages, number of CFT in each off-host life stage, and habitat type. Habitat types characterize the landscape in terms of good, fair, and poor habitats for ticks based on information provided by Teel et al. (1996, 1997). As applied in this study, and following Wang et al. (2016), mesquite constitutes good CFT habitat, mixed-brush constitutes fair CFT habitat, and uncanopied grass constitutes poor CFT habitat.

Temperature, saturation deficit, and precipitation index, climate variables known to affect survival, development, and oviposition rates of CFT (Mount et al. 1991, Davey et al. 1991), are included in the model to represent environmental conditions typical of South Texas (Figure 4.3). These variables are updated at the beginning of each week based on historical values obtained from the Southern Regional Climate Center (SRCC) Data Portal (SRCC 2019), using data from the Corpus Christi meteorological station, to parameterize climatic conditions typical of South Texas, in an area historically infested by CFT (Estrada-Peña et al. 2006b, Giles et al. 2014). Off-host development, survival, oviposition, and host-seeking rates of the various life stages of CFT are updated at the beginning of each week in each habitat type, based on these new environmental conditions and on life-history information obtained from Mount et al. (1991).

This hypothetical landscape, typical of south Texas (Archer et al. 1988), consists of 30% good habitat, 30% fair habitat, and 40% poor habitat. At the beginning of each simulation, each habitat cell is assigned 100,000 larvae. Each week, as a function of temperature, saturation deficit, and

precipitation (following Mount et al. [1991] and Cooksey et al. [1989]), the program calculates, for each habitat cell, the number of CFT in each stage of their life cycle that survive and develop into the next stage, the number of eggs laid, the number of off-host larvae that attach to each type of host, and the number of on-host adults dropped from each host.

The host community represents the characteristics of potential domestic and wild hosts across the landscape in terms density and use of space, based on movement rules and CFT burdens governed by host-specific attributes of size of activity range, habitat preferences, relative CFT carrying capacity, and the resulting change in attributes of landscape cells (collection of host-seeking larvae). The different host scenarios considered for simulations included cattle only (Cattle Only), cattle and WTD (C+WTD), and WTD only (WTD Only).

At the beginning of each simulation, the program creates individual (*Bos taurus*) and WTD hosts based on typical cattle stocking rates under continuous grazing (0.125 cattle/ha) and on WTD densities representative for South Texas (0.6175 WTD/ha) based on information presented by Cooper et al. (2008) and Kie and Bowyer (1999). At the beginning of each week, the program checks to see if CFT eradication (i.e., pasture vacation) should be applied and, if necessary, cattle are removed from a pasture for the course of 52 weeks. In each habitat cell, individual hosts have a probability of collecting CFT that depend on the abundance and activity level of host-seeking larvae, with an upper limit determined by the number of CFT already attached to that host.

Activity ranges and relative number of larvae that individual cattle and WTD hosts can carry at any given time are based on information presented by Howery et al. (1996), Cooksey et al. (1989),

and Hellickson et al. (2008). The duration of on-host life stages, the on-host survival rates, and the proportion of engorged adults that are deposited in each cell are based on Mount et al. (1991) and Wang et al. (2016). Hosts move across the landscape over the course of 30 weekly movements (potentially visiting 30 different, but not necessarily contiguous, habitat cells). After each round of 30 movements, the number of newly-acquired larvae is recorded (with the corresponding adjustment to the number of off-host larvae in the habitat cell), and the number of deposited engorged adult CFT in the habitat cell is recorded (with the corresponding adjustment to the number of on-host adult CFT; see Wang et al. 2016 for details).

I modified the model previously developed by Wang et al. (2016) by adding the flexibility to represent shifts in the habitat preferences of native hosts (i.e., WTD). The habitat preferences sub-model represents the rules governing the movement of ungulate hosts, and the duration of residence of cattle, which simulates the vacation of pastures as an eradication strategy for CFT. To develop the habitat preferences sub-model, I drew upon the model developed by Wang et al. 2016, with some modifications.

I used information from studies on forage preferences and dietary composition of cattle to assign their habitat-specific preference values, based on the idea that food preference is one of the several mechanisms shaping habitat use (Stuth 1991, Scott 1995). When dietary preferences values were not directly available, I estimated the percent composition of diets from information in the text or tables. The sources for this information, along with details on dietary preferences, location, and methods used in estimating diet composition are presented in Table 4.1.

Table 4.1. Dietary preferences of cattle, based on percent (%) composition of grass and browse, from year-round studies conducted across different locations in South Texas.

% Grass	% Browse	Method Used for Estimation of Dietary Composition	Source	Location
54.5	31.3	Bite counts	McMahan 1964	Kerr Wildlife Management Area
75.0	6.0	Bite counts; vegetation inventory	Drawe and Box 1968	Welder Wildlife Refuge
59.9	1.0	Esophageal fistulae	Ortega et al. 1997	Welder Wildlife Refuge
74.7	4.0	Fecal analysis; vegetation sampling	Everitt et al. 1981	Hidalgo County

Averaging the values shown in Table 4.1, grass and browse constitute approximately 60% and 10%, respectively, of cattle diets. I used these two values as proxies for their proportional preferences for uncanopied grass (preference = 0.6) and mixed-brush (preference = 0.1) habitats, while the remaining 30% represented cattle preference for mesquite habitat (preference = 0.3).

Using the information presented above, relative habitat preferences of cattle were kept constant for all the simulated scenarios at 0.3, 0.1, and 0.6 for good (i.e., mesquite), fair (i.e., mixed-brush), and poor (i.e., uncanopied grass) CFT habitats, respectively, as described and implemented by Wang et al. (2016).

WTD habitat preferences did not change during a simulation run, but to explore the influence of habitat preferences on CFT population dynamics, this sub-model allowed for WTD habitat preferences for good CFT habitat to change in 0.1-increments from 0 – 1 (i.e., from low to high preference for mesquite), with the remaining preference being split equally between the fair and poor habitats (i.e., mixed-brush and uncanopied grass).

The sizes of activity ranges (300 ha for cattle and 675 ha for WTD) were selected based on information in Howery et al. (1996) and Hellickson et al. (2008). The model selects probabilistically the center (*x,y* coordinates) of activity ranges during initialization, based on the habitat preferences of each host; subsequent habitat cells within the activity range are also selected probabilistically, based on the habitat preferences of the host (Figure 4.4). Hosts can move within their activity range 30 times per week; they choose available habitat cells based on their habitat preferences, but preferences are restricted by availability of habitats within each individual host's activity range.

The model was programmed in NetLogo (Wilensky 1999); simulations were executed and results were exported by NetLogo as Excel (Microsoft Excel 2016) text files for archiving and analyses. At the beginning of each simulation, the NetLogo program initializes the system by creating and assigning attributes to the landscape cells and individual hosts as described in the landscape and host sub-models; the program then reads time series of values for the climate variables described in the climate sub-model, and subsequently, the program iteratively executes the steps of the habitat preferences sub-model, 30 times per week, as shown in Figure 4.2. Weekly cohorts of CFT are tracked as they pass through the various life stages shown in Figure 4.3 (eggs, free-living larvae, on-host larvae, on-host nymphs, on-host adults, engorged adults).

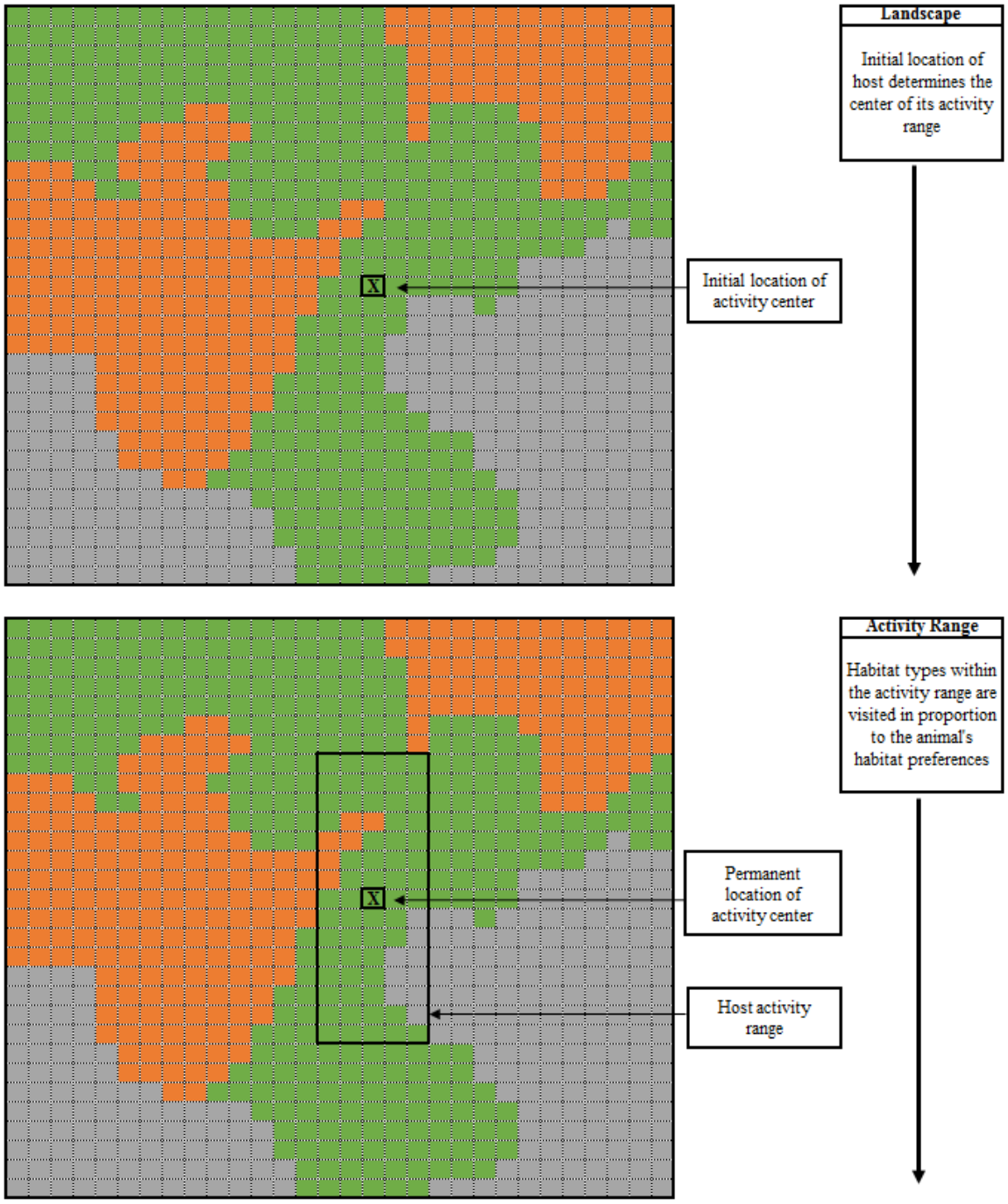

Figure 4.4. Schematic representation of the hierarchical relationships among landscape (top panel), activity range (middle panel), and weekly movements (bottom panel) that occur in the habitat-tick-host landscape interaction[1].

[1.] Colors represent the different habitats included in this model (orange = mesquite, gray = mixed-brush, green = uncanopied grass).

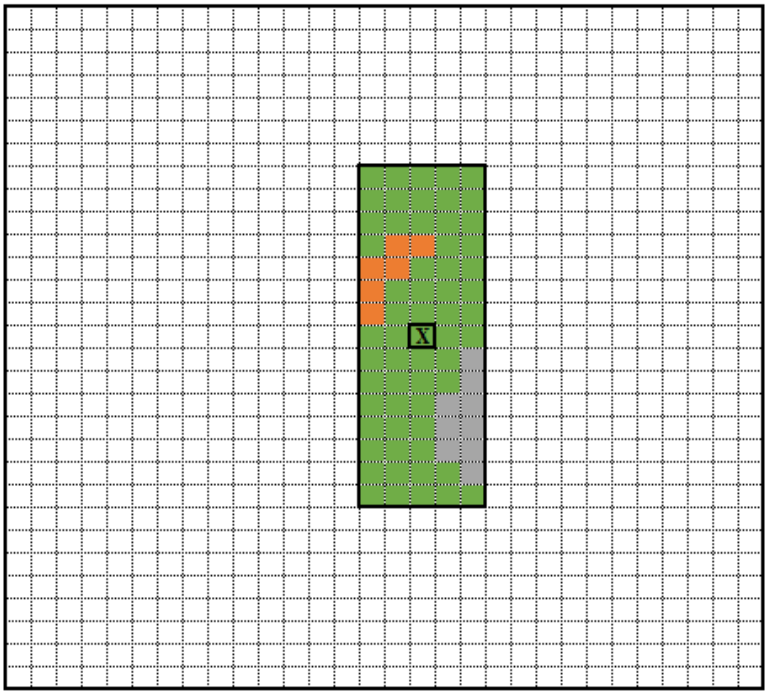

Figure 4.4. Continued.

4.2 Model Calibration

Wang et al. (2016) calibrated their model such that CFT populations survived on WTD, in the absence of cattle, in a hypothetical landscape representing pastures of mixed-rangeland consisting of 30% mesquite (good habitat for CFT), 30% mixed-brush (fair habitat for CFT), and 40% uncanopied grass (poor habitat for CFT).

One of the assumptions of my model was that CFT would be sustained in WTD Only simulations, under all the habitat, weather, and host community conditions considered in the model. Since the model presented here is largely based on the one developed by Wang et al. (2016), with the major difference being the host habitat preferences sub-model, I needed to determine the need for calibration such that my results would be similar to those presented by Wang et a. (2016). To this

end, a preliminary set of simulations was performed to determine whether CFT populations could be sustained under the most unfavorable conditions in terms of climate, habitat suitability, and available hosts.

4.3 Model Evaluation

Using the hypothetical 30% mesquite, 30% mixed-brush, and 40% uncanopied grass landscape, the model was evaluated by assessing the effect of WTD habitat preferences on the population dynamics of CFT under different host scenarios following a multi-step approach. The evaluation involved (a) verifying that host habitat preferences and movement rules included in the model generated the expected temporal patterns of host-seeking larvae and adult CFT under a wide range of conditions; (b) comparing simulated population-level CFT dynamics to patterns reported in the scientific literature; and (c) examining the sensitivity of simulated tick population size to changes in host habitat preferences.

To evaluate general performance, I ran a set of multi-year baseline simulations with densities of hosts, climatic conditions, and landscape composition representative of South-Texas rangelands, as described in the *"Model Description"* Section. To verify that the modified model still performed like the validated model of Wang et al. (2016), I compared their results to my model's output of the host-seeking larvae densities at the landscape level in Cattle Only, C+WTD, and WTD Only simulations. I used the hypothetical landscape described by Wang et al. (2016) to determine whether my model processes were producing patterns that characterized the system and whether the modifications related to WTD habitat preferences changed the system behavior.

Since a large amount of variability may cause the model's results to be questionable, with implications for the appropriateness of the model to accurately describe the habitat-tick-host system of interest, I conducted replications of the stochastic model by running 31 Cattle Only simulations over a 60-month period (from January 1995 – December 1998). I recorded weekly values of (1) the number of host-seeking larvae at the system level, (2) the number of host-seeking larvae by habitat type, (3) the number of engorged adults dropping from each type of host at the landscape level, and (4) the number of engorged adults dropping from each type of host at the habitat level, to determine the amount of stochastic variability in the model.

To examine how changes in habitat preferences of WTD affected the model results, I changed WTD habitat preferences for good CFT habitat in proportional increments from 0 (i.e., no preference for good CFT habitat) to 1 (complete preference for good CFT habitat), with the preferences for the other two habitat types (fair and poor CFT habitats) being split equally. I ran sets of 5 replicate stochastic (Monte Carlo) simulations for a period of 4 years to qualitatively (direction of outputs) and quantitatively (both directions and magnitudes of outputs) assess the effect of changes in habitat preferences upon the model's behavior. I recorded weekly values of (1) the number of host-seeking larvae at the landscape level, (2) the number of host-seeking larvae at the habitat level, (3) the number of engorged adults dropping from each type of host at the landscape level, and (4) the number of engorged adults dropping from each type of host at the habitat level.

4.4 Model Application

To explore the effect of WTD habitat preferences on the efficacy of pasture vacation as an eradication strategy for CFT infestations, I used an eradication scenario (Cattle Off) in which cattle

were removed from the system at the beginning of the year 1995 and were reintroduced at the beginning of the year 1996, corresponding to a period of 52 weeks. At the end of the eradication protocol, the system was restocked with the same number of cattle present before the pasture vacation. I ran sets of 5 replicate stochastic simulations of each of several versions of this Cattle Off eradication scenario in which I evaluated response of CFT populations to the interactions of cattle and WTD, assuming different WTD habitat preferences but keeping cattle preferences constant at 0.3, 0.1, and 0.6 for mesquite, mixed-brush, and uncanopied grass, respectively. As with the previous host scenarios, the simulation period spanned 4 years (1995 – 1998) under climatic and landscape conditions typical of South Texas.

The combination of changes in WTD habitat preferences (preferences for mesquite varied from 0 – 1 in increments of 0.1) and host species present (C+WTD, WTD Only, and Cattle Off) resulted in 33 sets of simulations during which I monitored (1) the relative density of host-seeking larvae at the landscape level (i.e., off-host larvae in the landscape), (2) the relative density of host-seeking larvae at the habitat level, (3) the number of adult CFT on cattle at the landscape level, (4) the number of adult CFT on cattle at the habitat level, (5) the number of adult CFT on WTD at the landscape level, and (6) the number of adult CFT on WTD at the habitat level.

To assess the efficacy of the pasture vacation in controlling CFT infestations, I focused on the details of the CFT population dynamics during the recovery period using several "recovery indexes" including (a) recovery period (i.e., number of weeks necessary to reach at least 60% of the pre-treatment host-seeking larvae density), (b) mean number of host-seeking larvae weeks (i.e., area under the curve of host-seeking larvae densities over the course of the recovery period), and

(c) minimum and maximum host-seeking larvae average densities (i.e., mean number of host-seeking larvae/ha at the beginning and the end of the recovery period).

5 RESULTS

5.1 Model Calibration

CFT were able to survive under the most unfavorable conditions, in a landscape composed entirely of poor habitat for ticks consisting of 0% mesquite, 0% mixed-brush, and 100% uncanopied grass, with WTD as the only host available (i.e., WTD Only simulations), and subject to a wide range of non-catastrophic environmental conditions (Figure 5.1). This result indicated that recalibration of the model already calibrated by Wang et al. (2016) was not necessary since the model was producing the results expected based on the assumption of CFT populations surviving under the WTD Only simulation.

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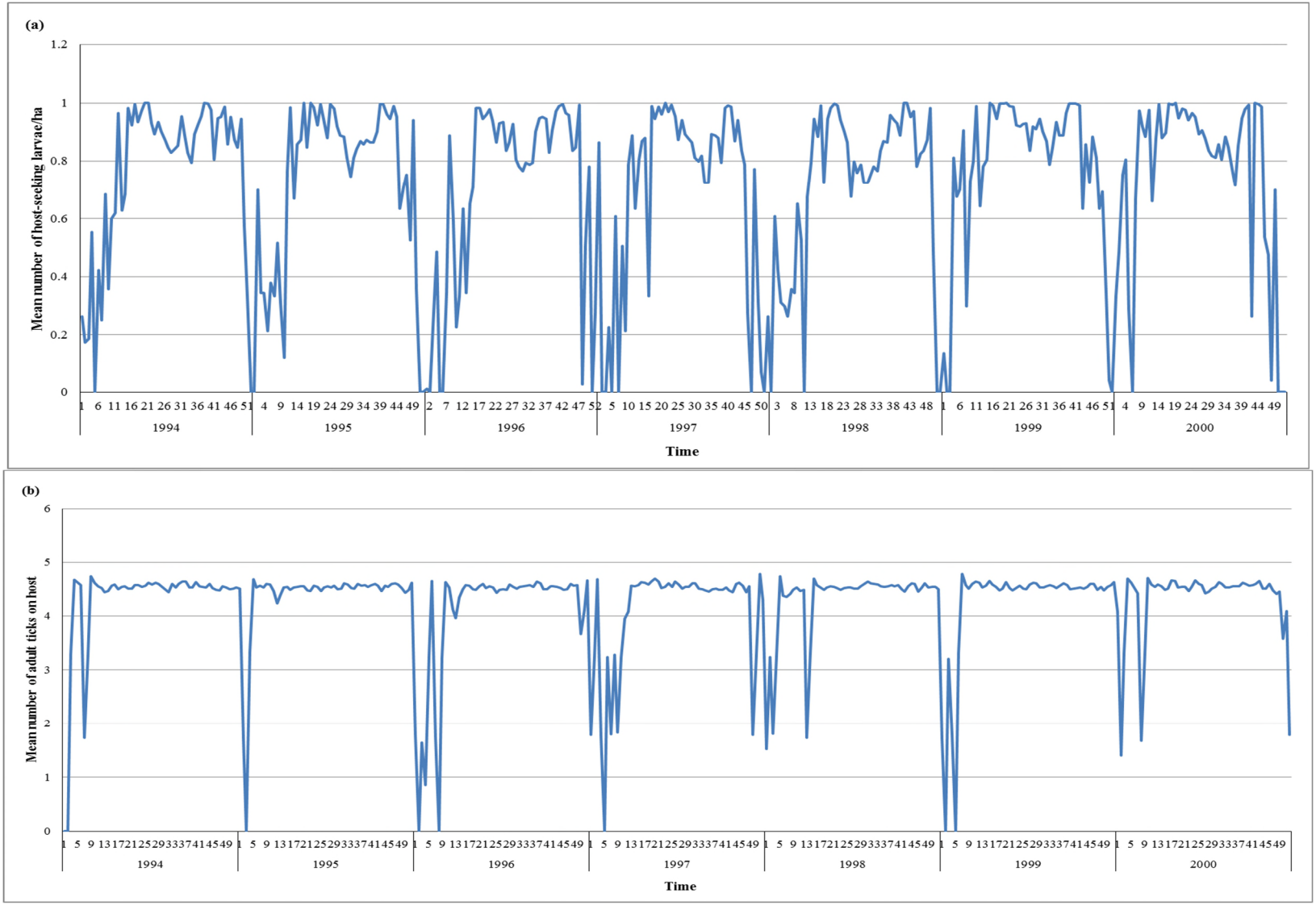

Figure 5.1.Response of (a) host-seeking larvae and (b) adult cattle-fever ticks on white-tailed deer (WTD) to weather dynamics under unfavorable landscape (100% uncanopied grass) and host (white-tailed deer only) conditions.

5.2 Model Evaluation

The usefulness of the model was evaluated for assessing the effect of WTD habitat preferences on the population dynamics of CFT and the effectiveness of eradication strategies following the multi-step approach described in the *"Methods"* Section.

To determine a simulation period adequate for the objectives of this study, I monitored the dynamics of host-seeking larvae and adult ticks both at the landscape and at the habitat level, over a period of 7 years (i.e., January 1994 – December 2000), which corresponded to the simulation period used by Wang et al. (2016). The response of the tick populations to the environmental and host community conditions considered during my simulations did correspond with the dynamics reported by Wang et al. (2016). Since the system reached equilibrium at the beginning of the second year (year 1995; Figure 5.2), I decided to run all the simulations used for this study over a period of 4 years (i.e., 1995 – 1998) instead of the 7 years used by Wang et al. (2016). I considered this period was adequate for all aspects of model evaluation since it allowed enough time for the tick populations to respond to the different host scenarios being simulated.

Host-seeking larvae densities exhibited oscillations consistent with responses to the climate variables included in the model; 31 replicate stochastic simulations of the Cattle Only scenario were conducted to measure the variability of host-seeking larvae through the simulation time (Figure 5.3). These results of these simulations were consistent across replicates at the landscape level and no significant differences ($p > 0.05$) among different replicates were detected, indicating low stochastic variability in the dynamics of CFT throughout the 4-year simulation period (Figure 5.3).

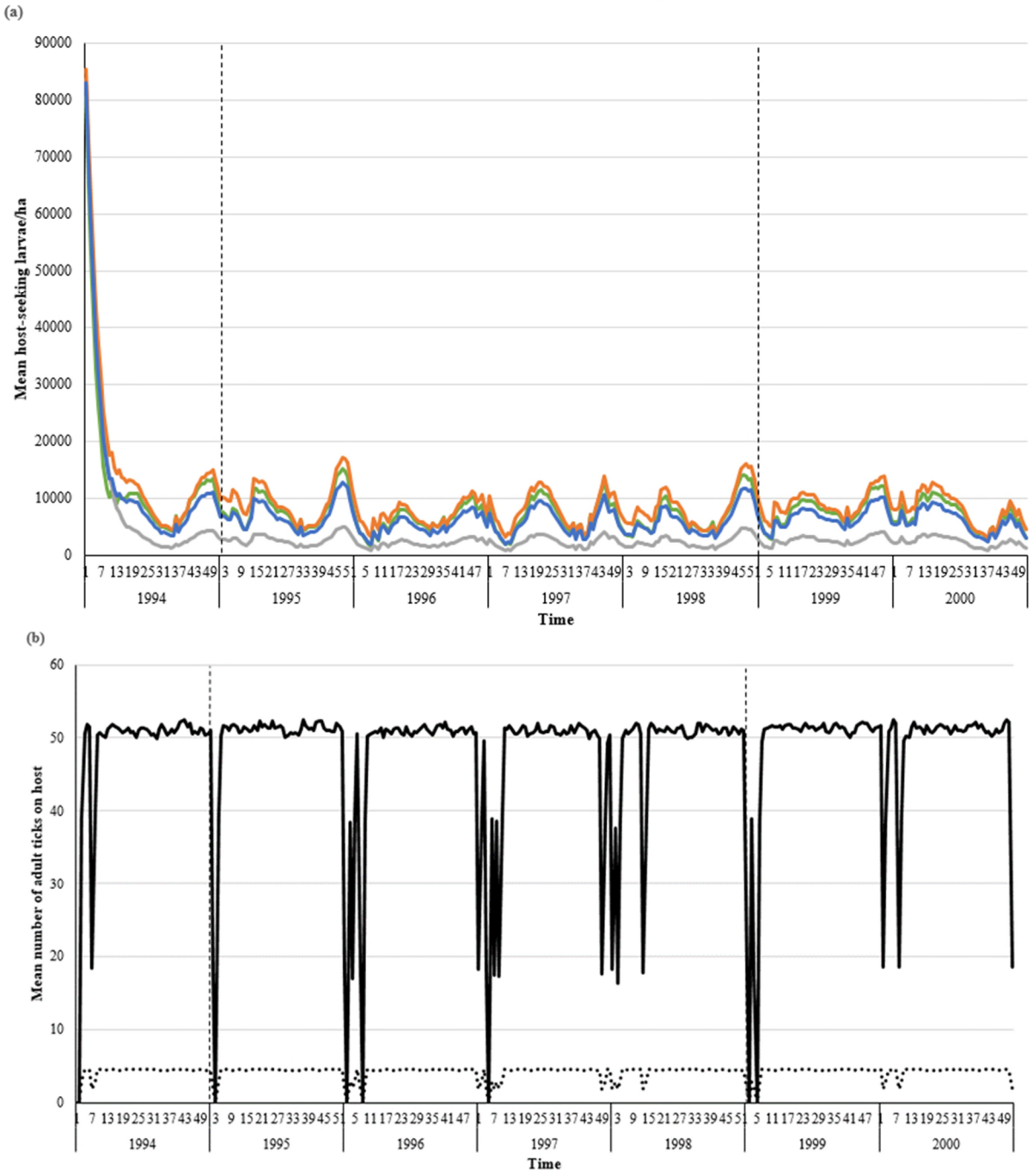

Figure 5.2. Seven-year[1] population dynamics of a) host-seeking larvae[2] and b) adult cattle-fever ticks[3] under conditions of weather (temperature, saturation deficit, and precipitation index), host community (cattle and white-tailed deer), and habitat (mesquite, mixed-brush, and uncanopied grass) typical of South-Texas arid rangelands.

[1.] Vertical dashed lines represent the 4-year period selected for evaluation and application of my model.

[2.] Mean number of host-seeking larvae at the landscape level (blue line), and habitat level (orange = mesquite; gray = mixed-brush; green = uncanopied grass).

[3.] Mean number of adult ticks on cattle (solid line) and white-tailed deer (dotted line)

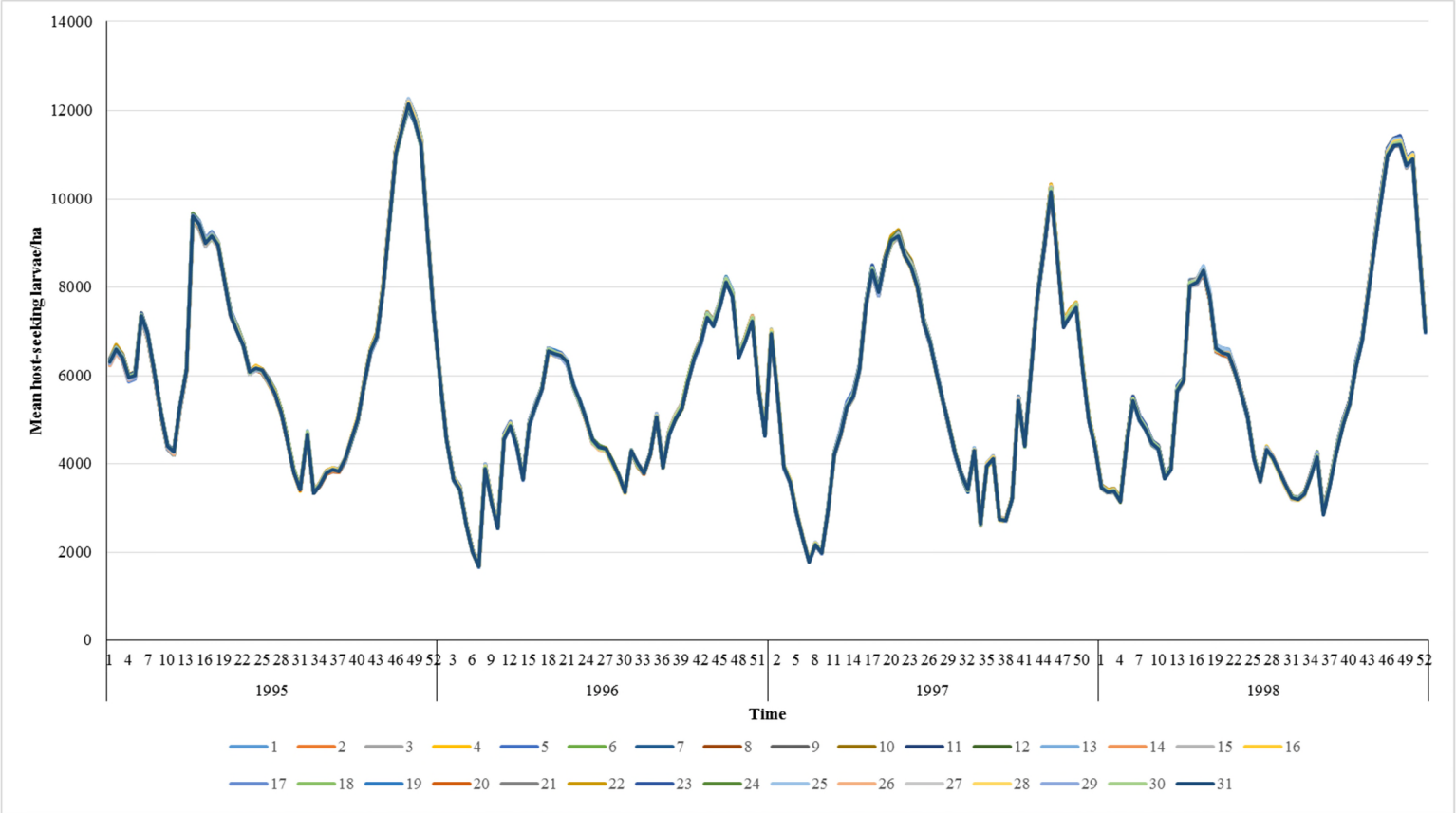

Figure 5.3. Landscape-level temporal trends in mean densities of host-seeking larvae populations of cattle-fever ticks for all the 31 replicates1 of the simulations in which cattle were the only host present in the system.

[1.] Colored lines represent each of the 31 replicates ran for this simulation.

The system behaved as expected based on the dynamics of adult ticks on cattle and WTD at the landscape level (Figure 5.4), showing temporal changes in adult tick densities comparable in magnitude and direction to those reported by Wang et al. (2016). Numbers of adult CFT on cattle were higher than those on WTD and reached maximum and minimum numbers based on the tick carrying capacity of each host species and seasonal changes in climatic conditions.

The mean number of adult ticks on hosts varied seasonally, ranging from approximately 0 – 50, while the number of adult ticks on WTD ranged from 0 – 4.5 (Figure 5.4). The mean number of on-host adult ticks reached a plateau as it approached the maximum number of ticks that ungulate hosts could carry, and declines in infestations for each host species corresponded to the winter months, with the magnitude of these declines being influenced by variation in climatic conditions, in agreement with the results presented by Wang et al. (2016).

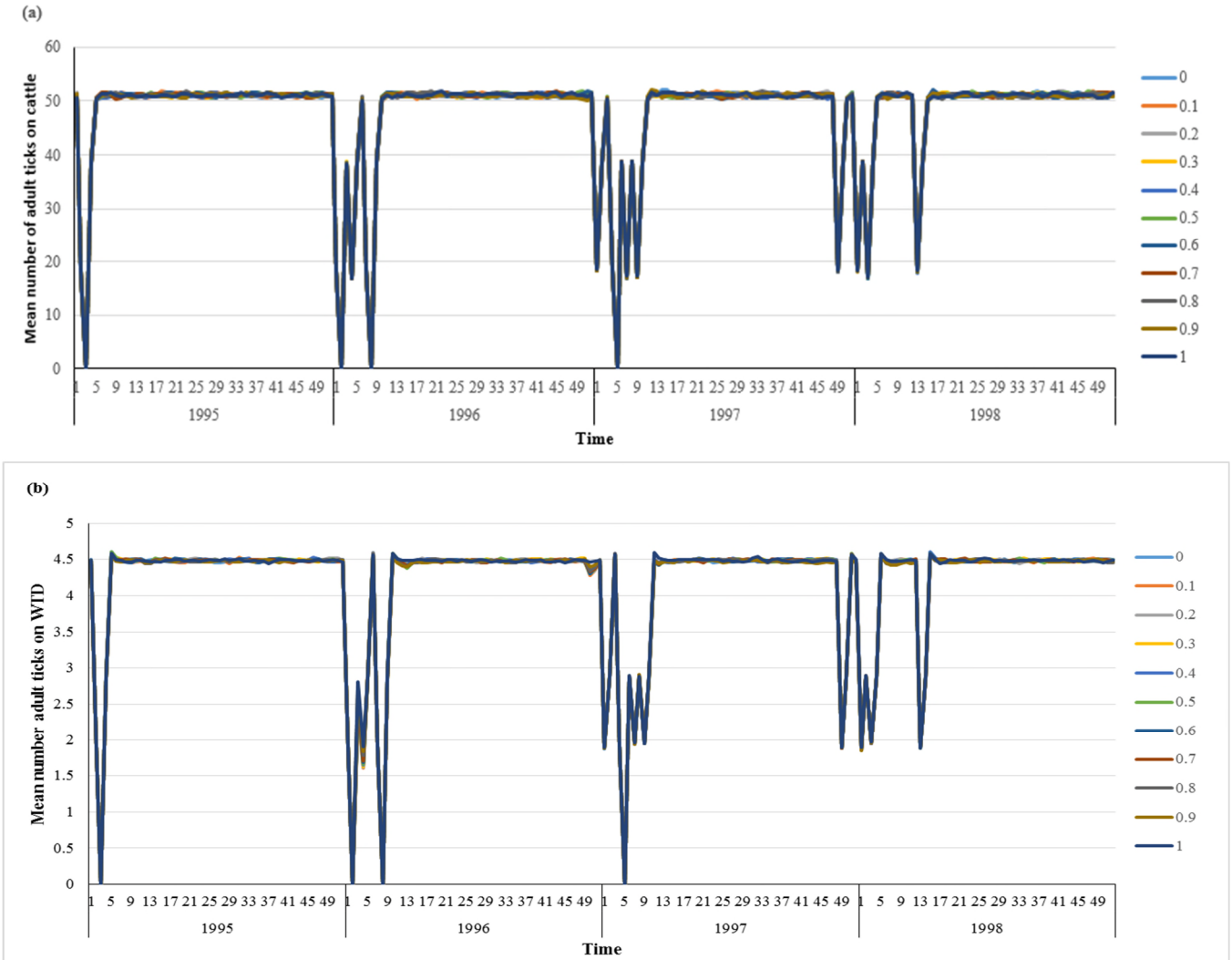

Figure 5.4. Landscape-level temporal trends in mean densities of adult cattle-fever ticks on (a) cattle and (b) white-tailed deer (WTD) for simulations in which both cattle and WTD were present and changes in WTD habitat preferences[1] (colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

The number of engorged adults dropped from each host into the landscape responded as expected to temporal changes in climate variables. Changes in habitat preferences did not have a visible effect on engorged adult ticks at the landscape level (Figure 5.5), as expected due to the short-lived nature of this free-living stage in the life cycle of CFT.

At the habitat level, the density of engorged adults dropped from cattle changed among habitat types for simulations in which habitat preferences for WTD varied from 0 – 1 and where both cattle and WTD were present (Figure 5.6), being the lowest in mixed-brush, as expected due to the low habitat preferences of cattle for this habitat. Within each habitat type, densities of engorged adult ticks were similar for simulations in which habitat preferences for WTD varied from 0 – 1, and where both cattle and WTD were present. However, where differences were more evident was in mixed-brush (Figure 5.6), the least preferred habitat by cattle (cattle preference for mixed brush was set at 0.1).

The results of the temporal trends of engorged adult densities indicated that regardless of WTD habitat preferences, the vast majority of engorged adults dropped into uncanopied grass came from cattle, as expected due to their high preference for this habitat type and their higher tick burdens.

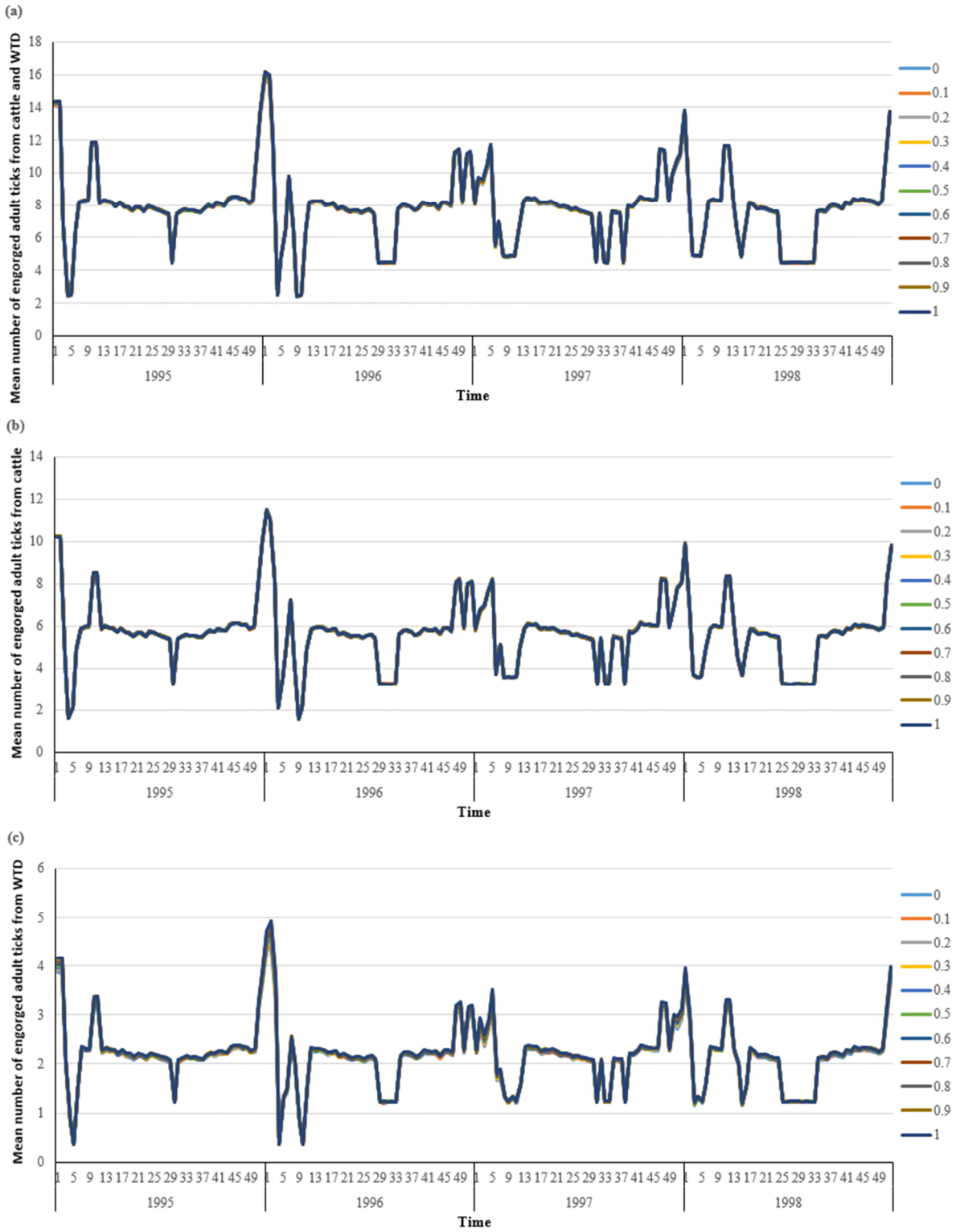

Figure 5.5. Landscape-level temporal trends in mean densities of engorged adult cattle-fever ticks dropped to the landscape from (a) both hosts, (b) cattle and (c) white-tailed deer (WTD) during simulations in which both cattle and WTD were present and changes in WTD habitat preferences[1] (colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

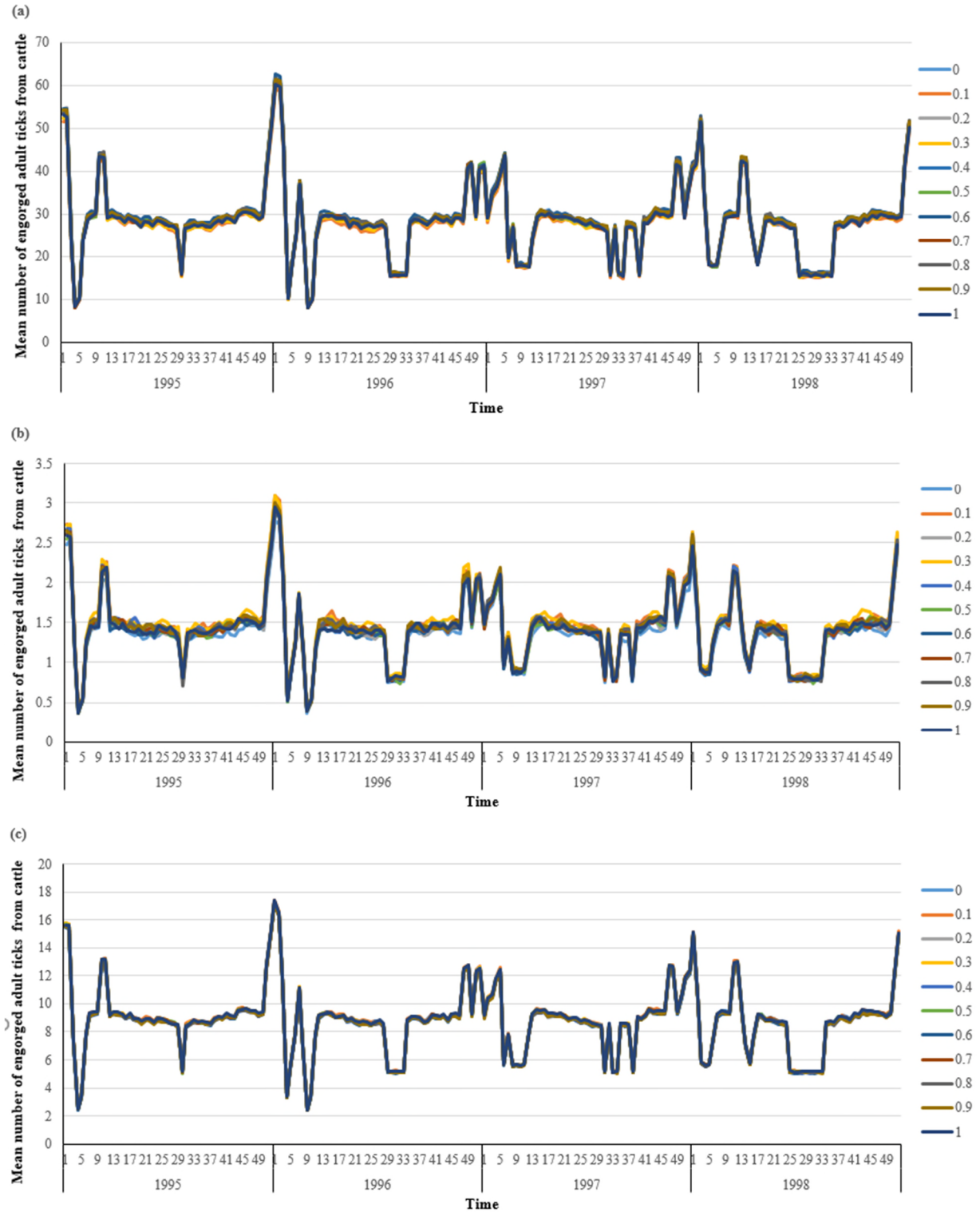

Figure 5.6. Habitat-level temporal trends in mean densities of engorged adult cattle-fever ticks dropped from cattle on (a) mesquite, (b) mixed brush, and (c) uncanopied grass, during simulations in which both cattle and white-tailed deer (WTD) were present and changes in WTD habitat preferences[1] colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

Densities of engorged adult ticks dropped from WTD within each habitat changed with changes in WTD habitat preferences (Figure 5.7). As expected, engorged adult ticks from WTD reached higher densities in mesquite (good CFT habitat), independent of WTD habitat preferences, increasing as WTD habitat preference for that habitat increased (Figure 5.7). Densities of engorged adult ticks dropped from WTD were the lowest in uncanopied grass, independent of habitat preferences, and decreased as WTD habitat preference for mesquite increased, as expected (Figure 5.7). Similar densities and trends to those shown in Figure 5.7 were observed with different host scenarios (i.e., WTD Only and Cattle Only).

The population dynamics of on-host adult ticks and engorged adult ticks provided relevant information regarding tick burdens and the role of each host species in distributing adult CFT across the landscape. However, from this point on, I will focus on host-seeking larvae, as this is the life stage where the dynamics and maintenance of tick infestations is more evident, due to the potential duration of this stage, as previously mentioned.

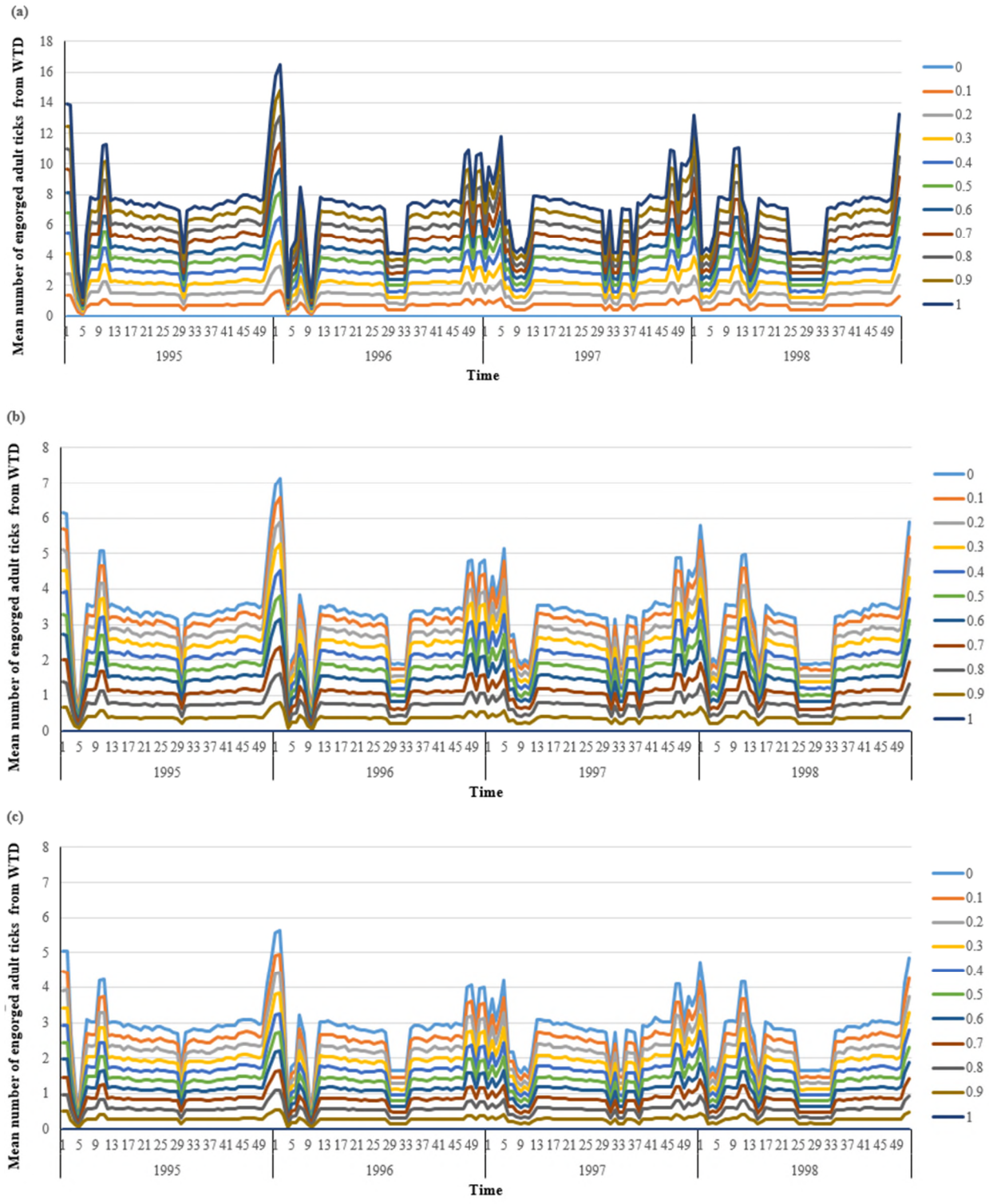

Figure 5.7. Habitat-level temporal trends in mean densities of engorged adult cattle-fever ticks dropped from white-tailed deer (WTD) on (a) mesquite, (b) mixed brush, and (c) uncanopied grass, during simulations in which both cattle and WTD were present and changes in WTD habitat preferences[1] (colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

The dynamics of host-seeking larvae through time at the landscape level, for simulations in which both cattle and WTD were present and changes in habitat preferences were included, reflected the seasonality imposed by environmental conditions on the tick populations (Figure 5.8). These results were in agreement with those obtained by habitat type (Figure 5.9) and with the results presented by Wang et al. (2016), indicating that this modified model is behaving as expected, maintaining CFT populations according to the particular combinations of climatic conditions and habitat preferences on a case by case basis.

Host-seeking larvae densities at the landscape level (Figure 5.8) fell within the maximum and minimum values of densities recorded at the habitat level (Figure 5.9), indicating that the system was behaving as expected. Mixed-brush (fair habitat for ticks) consistently supported the lowest densities of host-seeking larvae; this was also the habitat type where the largest differences in host-seeking larvae densities were observed across WTD habitat preferences (Figure 5.9), despite cattle preference for mixed-brush (0.1) being constant across simulations.

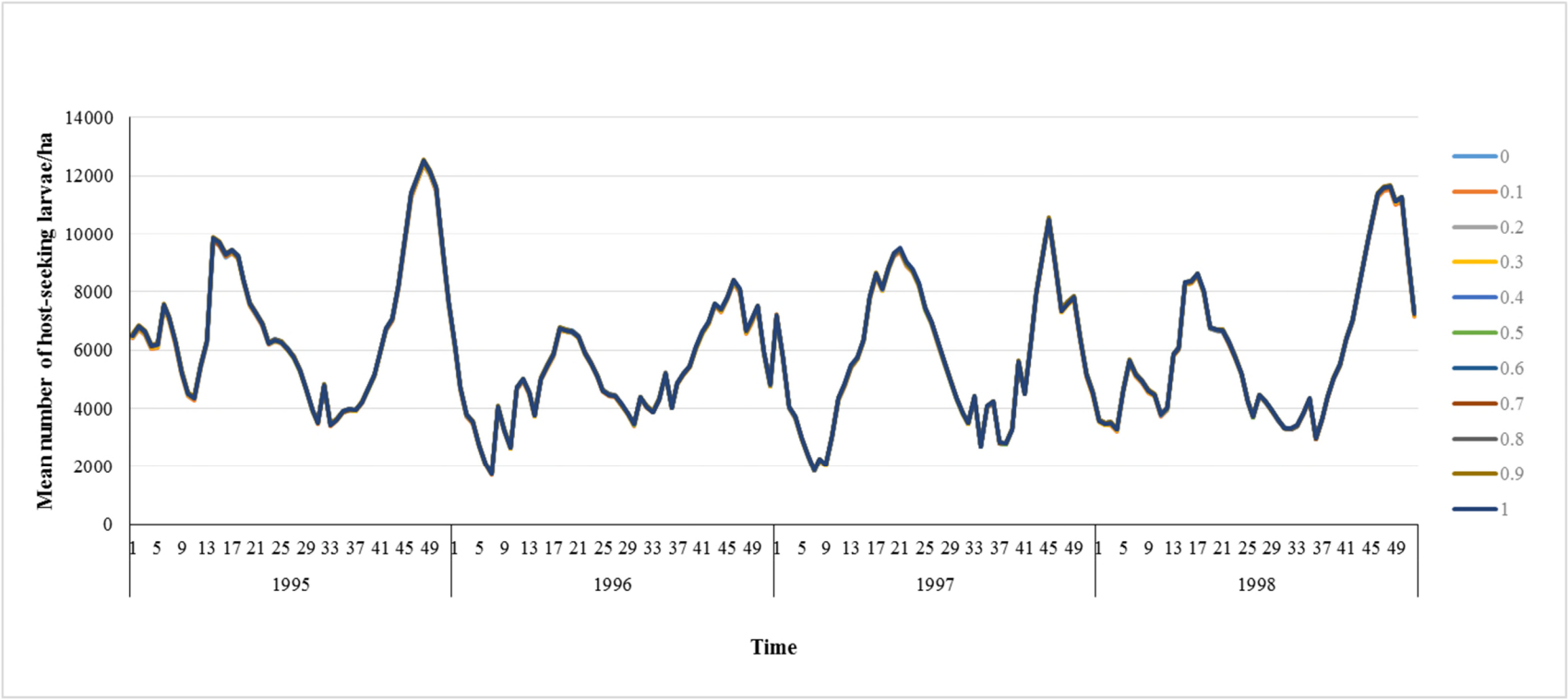

Figure 5.8. Landscape-level temporal trends in mean densities of host-seeking larvae populations of cattle-fever ticks for simulations in which both cattle and white-tailed deer (WTD) were present and changes in WTD habitat preferences[1] (colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

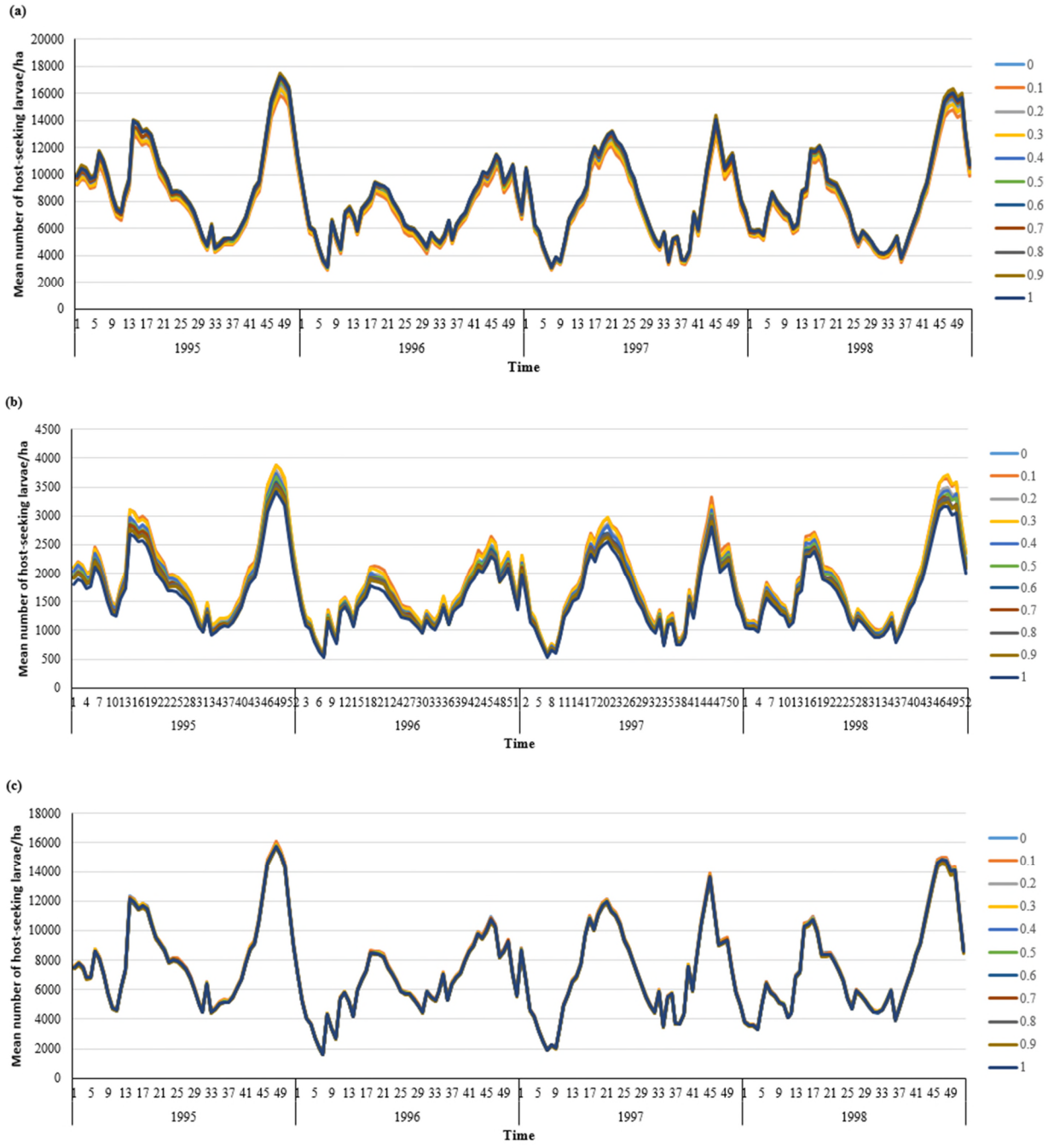

Figure 5.9. Habitat-level temporal trends in mean densities of host-seeking larvae populations of cattle-fever ticks on (a) mesquite, (b) mixed brush, and (c) uncanopied grass during simulations in which both cattle and white-tailed deer (WTD) were present and changes in WTD habitat preferences[1] (colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

Differences in host-seeking larvae at the landscape level were not evident for simulations in which both cattle and WTD were present and differences in habitat preferences were included (Figure 5.8); however, at the individual habitat level, differences in densities of host-seeking larvae for changes in habitat preferences were noticeable (Figure 5.9), especially in mixed-brush. Additionally, for a given value of WTD habitat preference, the density of host-seeking larvae increased in mesquite and decreased in uncanopied grass, as expected.

For simulations in which both cattle and WTD were present and differences in habitat preferences were included, temporal trends in host-seeking larvae densities in mesquite (good habitat for ticks) and uncanopied grass (poor habitat for ticks; Figure 5.9) matched closely with the temporal trends observed at the landscape level (Figure 5.8). Furthermore, differences in host-seeking larvae densities were less evident in uncanopied grass (the habitat more preferred by cattle but also the poor quality habitat in terms of CFT survival) compared to any other habitat type.

Landscape-level densities of host-seeking larvae for C+WTD simulations (Figure 5.8) followed similar trends to those observed for Cattle Only simulations (Figure 5.10), while CFT densities for WTD Only simulations (Figure 5.11) were evidently lower than to those reached under C+WTD or Cattle Only simulations.

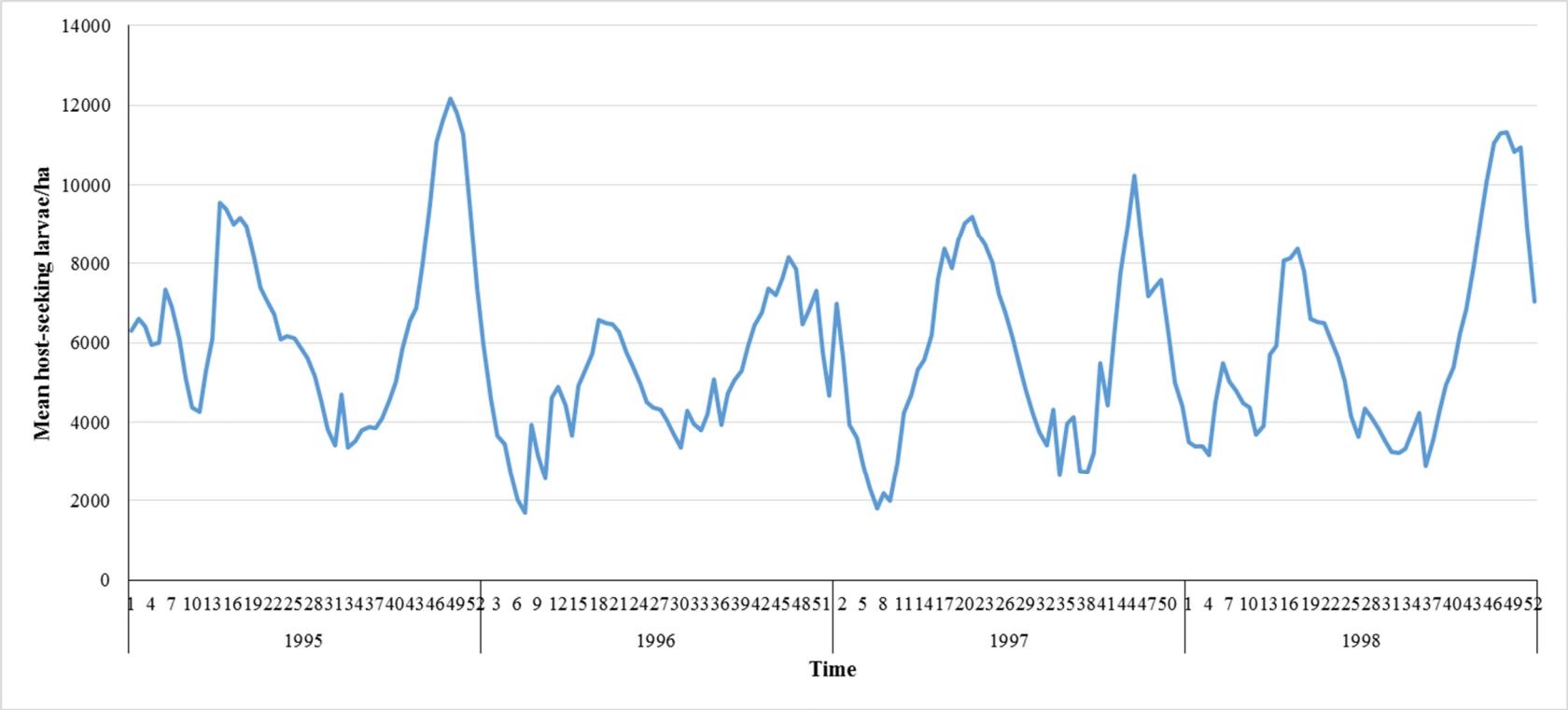

Figure 5.10. Landscape-level temporal trends in mean densities of host-seeking larvae populations of cattle-fever ticks for simulations in which only cattle were present.

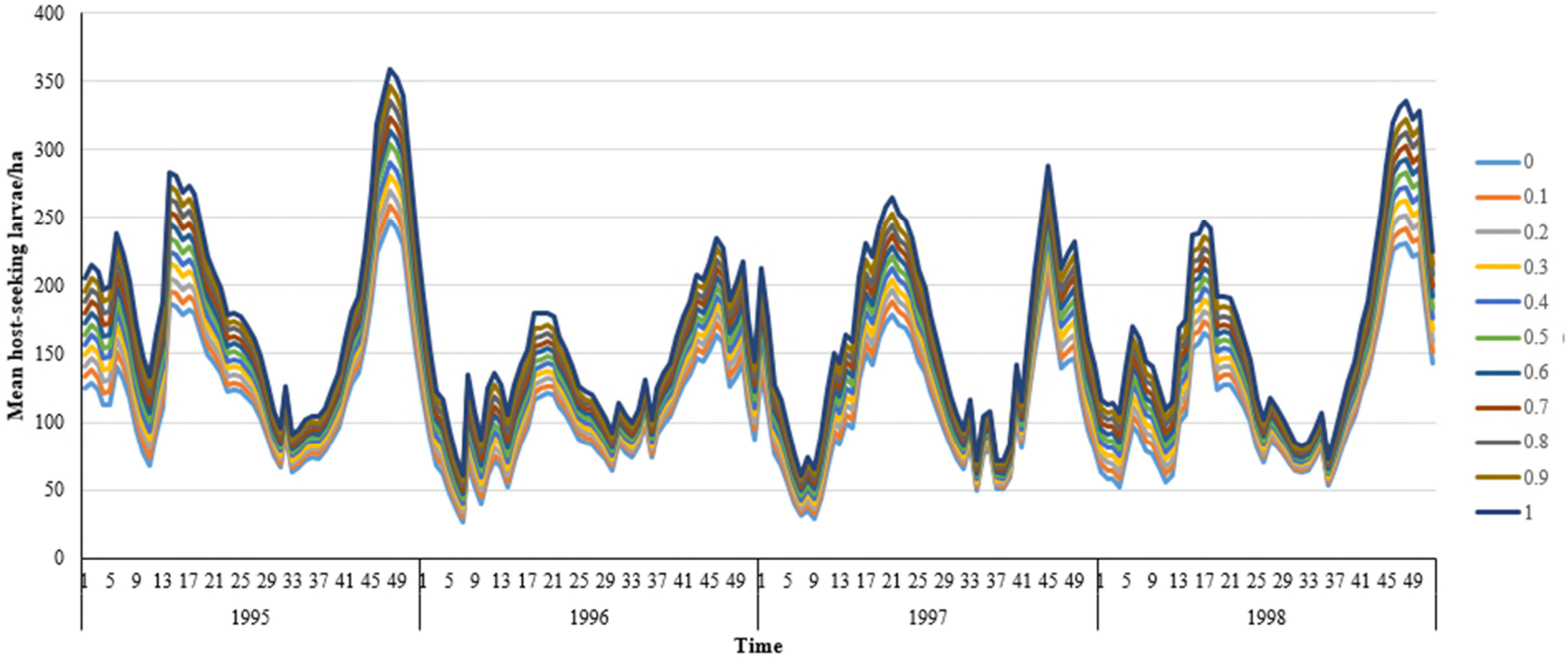

Figure 5.11. Landscape-level temporal trends in mean densities of host-seeking larvae populations of cattle-fever ticks for simulations in which only white-tailed deer (WTD) were present and changes in WTD habitat preferences[1] (colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

At the habitat level, the results of higher densities of host-seeking larvae in uncanopied grass compared to mixed-brush and mesquite made sense due to a higher use of uncanopied grass by cattle, determined by their habitat preferences. Densities of host-seeking larvae were similar between the habitat types preferred by cattle (i.e., mesquite and uncanopied grass) and the landscape-level densities, for simulations in which both cattle and WTD were present and where differences in WTD habitat preferences were included (Figure 5.12). On the other hand, host-seeking larvae densities across different preferences of WTD were much lower within the habitat type least preferred by cattle (i.e., mixed-brush), suggesting a spatial component in the role of WTD in sustaining CFT populations.

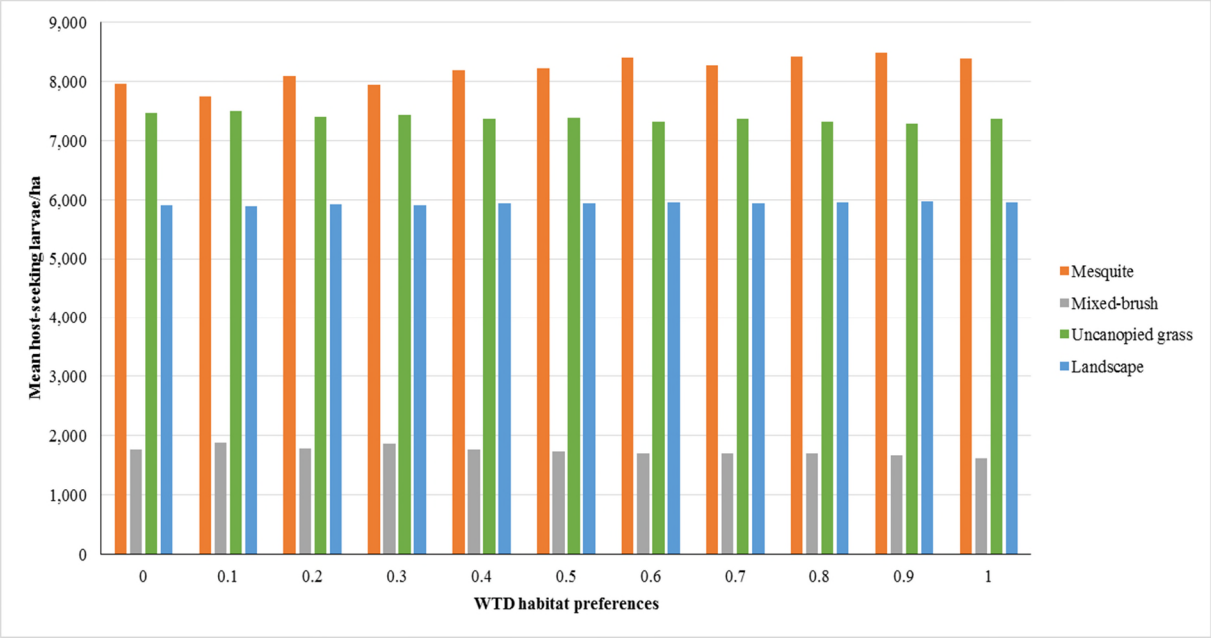

Figure 5.12. Landscape- and habitat-level mean densities of host-seeking larvae of cattle-fever ticks, across values of white-tailed deer (WTD) habitat preference, for simulations in which both cattle and WTD were present and changes in WTD habitat preferences[1] were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

Habitat-level densities of host-seeking larvae for the Cattle Only simulations (Figure 5.13) followed similar trends to the C+WTD simulations (Figure 5.9). On the other hand, for WTD Only simulations, CFT densities were not only consistently lower across habitats, but also showed evident differences within habitat types across different habitat preferences (Figure 5.14). In the absence of cattle, densities of host-seeking larvae within each habitat varied across the different values of habitat preferences, ranging from 0 – 1,200 host-seeking larvae/ha in mesquite, from 0 – 450 in mixed-brush, and from 0 – 275 in uncanopied grass (Figure 5.14).

Based on the results for the population dynamics of adult CFT on hosts, engorged adult CFT from hosts, and host-seeking larvae, my modified model is behaving as expected. The movement rules and habitat preferences built within the model structure influenced how much time the different host species were spending within each habitat; the climatic conditions and habitats influenced survival and development of CFT; and the use of space and maximum tick burdens for each host species influenced the dynamics of CFT populations, both at the landscape and at the habitat levels.

Within the context of the model's structure, the model was parameterized in such a way that cattle were able to host a higher number of ticks (10 times more) than WTD, and although WTD stocking rates (0.6175 individuals/ha) were higher than cattle stocking rates (0.125 individuals/ha), cattle were still able to carry a higher number of on-host adults (0.125*10 = 1.25) than WTD (0.61*1 = 0.61), moving CFT across the landscape disproportionately among their preferred habitats (i.e., uncanopied grass). Numerically, the model behaved as expected based on the rules imposed on the simulated system as part of the model's structure.

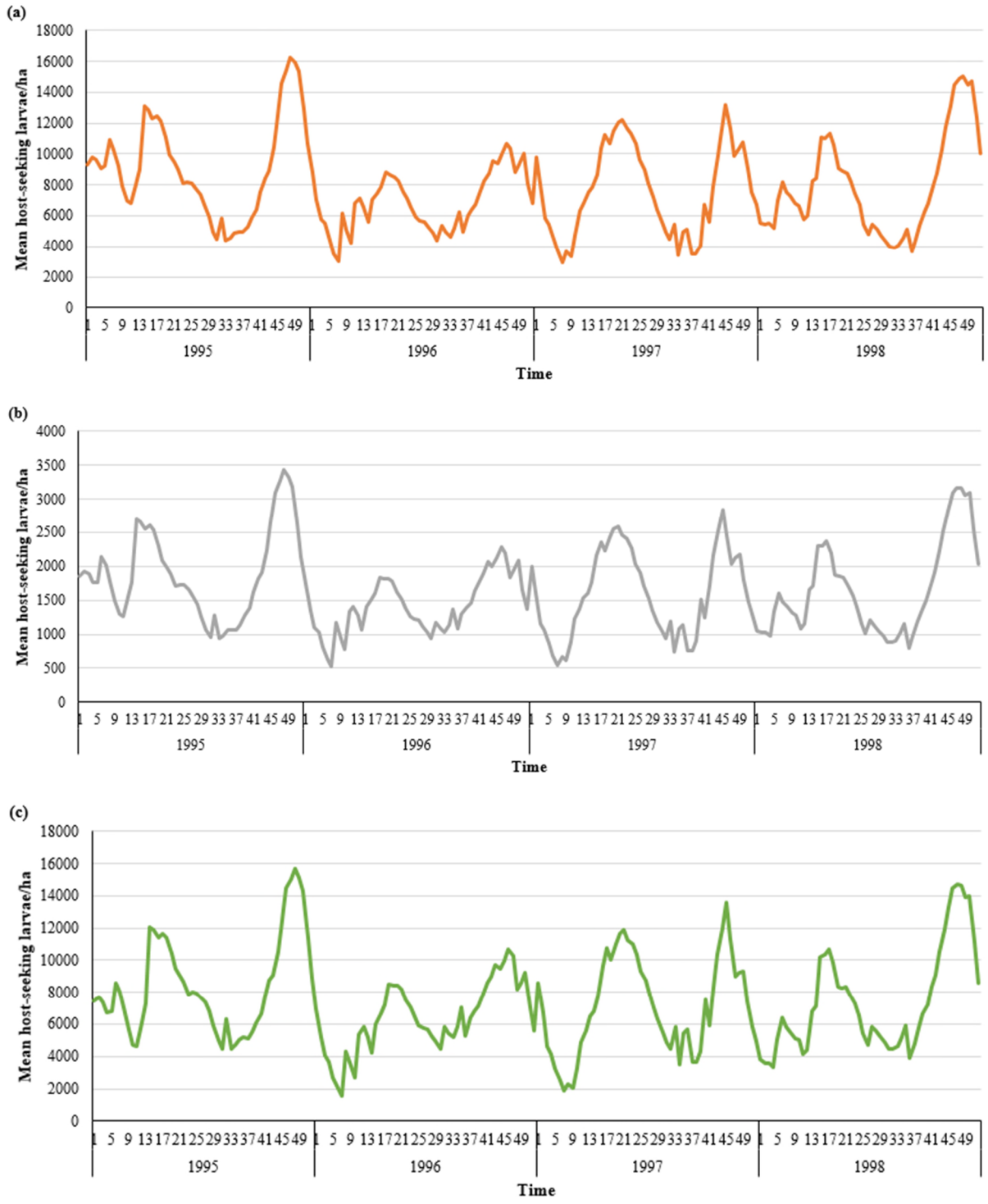

Figure 5.13. Habitat-level temporal trends in mean densities of host-seeking larvae populations of cattle-fever ticks on (a) mesquite, (b) mixed brush, and (c) uncanopied grass during simulations in which only cattle were present.

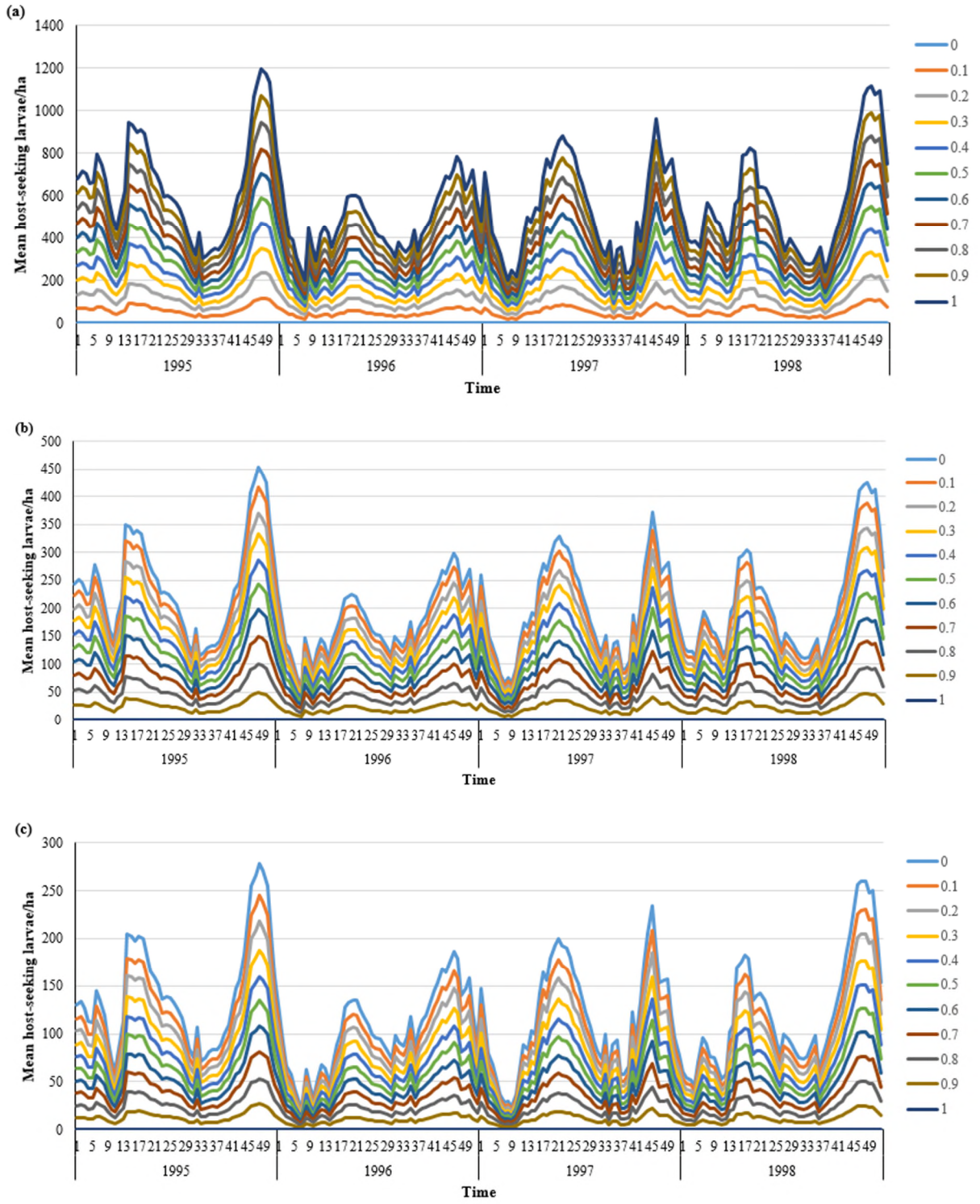

Figure 5.14. Habitat-level temporal trends in mean densities of host-seeking larvae populations of cattle-fever ticks on (a) mesquite, (b) mixed brush, and (c) uncanopied grass during simulations in which only white-tailed deer (WTD) were present and changes in habitat preferences[1] of WTD (colored lines) were included.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

After a careful inspection of the model output, these results confirmed that the modified model was behaving as expected. Relative differences in the densities of CFT across habitat types and WTD habitat preferences were reasonable and corresponded with the expected general patterns of a multi-host system in a semi-arid landscape. On the basis of the evaluation process, this model seems a potentially useful tool for the study of CFT populations and the role of WTD habitat preferences on the effectiveness of eradication strategies.

5.3 Model Application

The removal of cattle from the system for 52 consecutive weeks (i.e., pasture vacation during the year 1995 or Cattle Off), starting the first week in January of 1995, was conducted to assess the effect of WTD habitat preferences on the efficacy of CFT eradication strategies.

The results from the Cattle Off scenario (Figure 5.15) showed that cattle filled up with adult CFT quickly after the conclusion of the 52-week long eradication protocol, reaching pre-treatment CFT loads (approximately 51 adult ticks) by week 17 of 1996. WTD sustained pre-treatment (Figure 5.4) CFT loads and filled up with CFT even in the absence of cattle (Figure 5.15), in agreement with the results reported by Wang et al. (2016), whose model development included a calibration factor to limit the maximum number of adult ticks that individual hosts could carry at any given time. The mean number of adult CFT on WTD ranged from 0 – 4.6 at the landscape level; these tick loads seemed to be less susceptible to the presence (or absence) of cattle than to changes in habitat preferences.

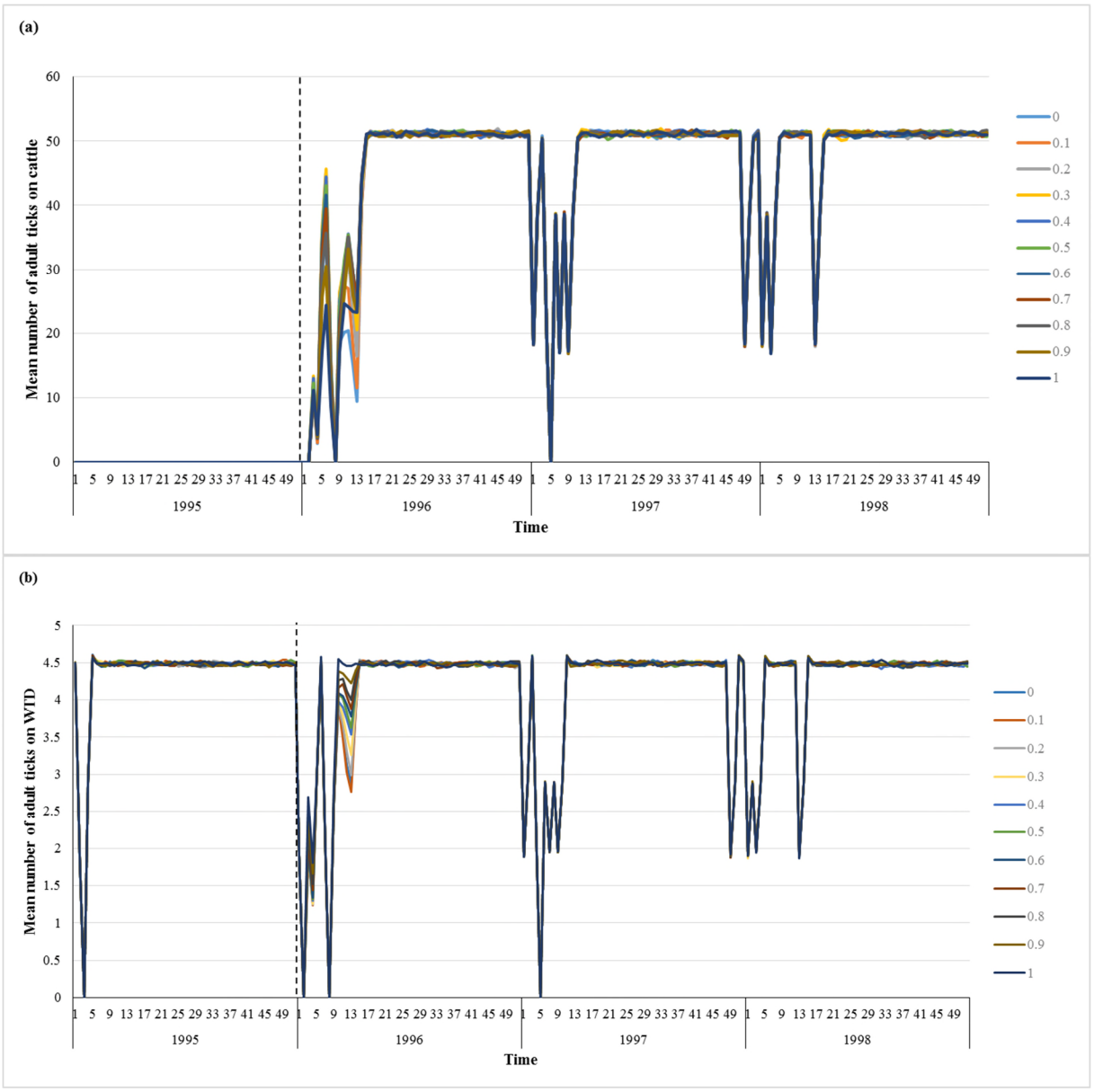

Figure 5.15. Landscape-level temporal trends in mean densities of adult cattle-fever ticks on (a) cattle and (b) white-tailed deer (WTD) for simulations in which cattle vacated the system for a period of 52 weeks[1] and changes in habitat preferences of WTD[2] (colored lines) were included.

[1.] Dashed vertical line represents the end of the 52-week long eradication protocol (Cattle Off).

[2.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

The population dynamics of on-host adult ticks provided relevant information regarding tick burdens and the role of each host species in distributing adult ticks across the landscape; however, from this point on, I will focus on host-seeking larvae, as this is the life stage where the dynamics and maintenance of tick infestations is more evident, as previously mentioned.

The Cattle Off treatment substantially suppressed the number of host-seeking larvae at the landscape level for all values of WTD habitat preferences, ranging from 18.4 – 50.6 host-seeking larvae/ha, for preferences 0 and 1, respectively (Figure 5.16). However, despite greatly reducing the number of host-seeking larvae, the system remained infested throughout the duration of the eradication protocol (i.e., 52 weeks), and tick populations started to recover relatively quickly after the end of the pasture vacation period (week 10 of 1996; Figure 5.16). Within 23 weeks of termination of the cattle vacation, CFT infestations at the landscape level reached approximately 62% of the pre-treatment densities, and within a year, the CFT populations were back in equilibrium with pre-treatment dynamics (Figure 5.16). These results are consistent with those reported by Wang et al. (2016).

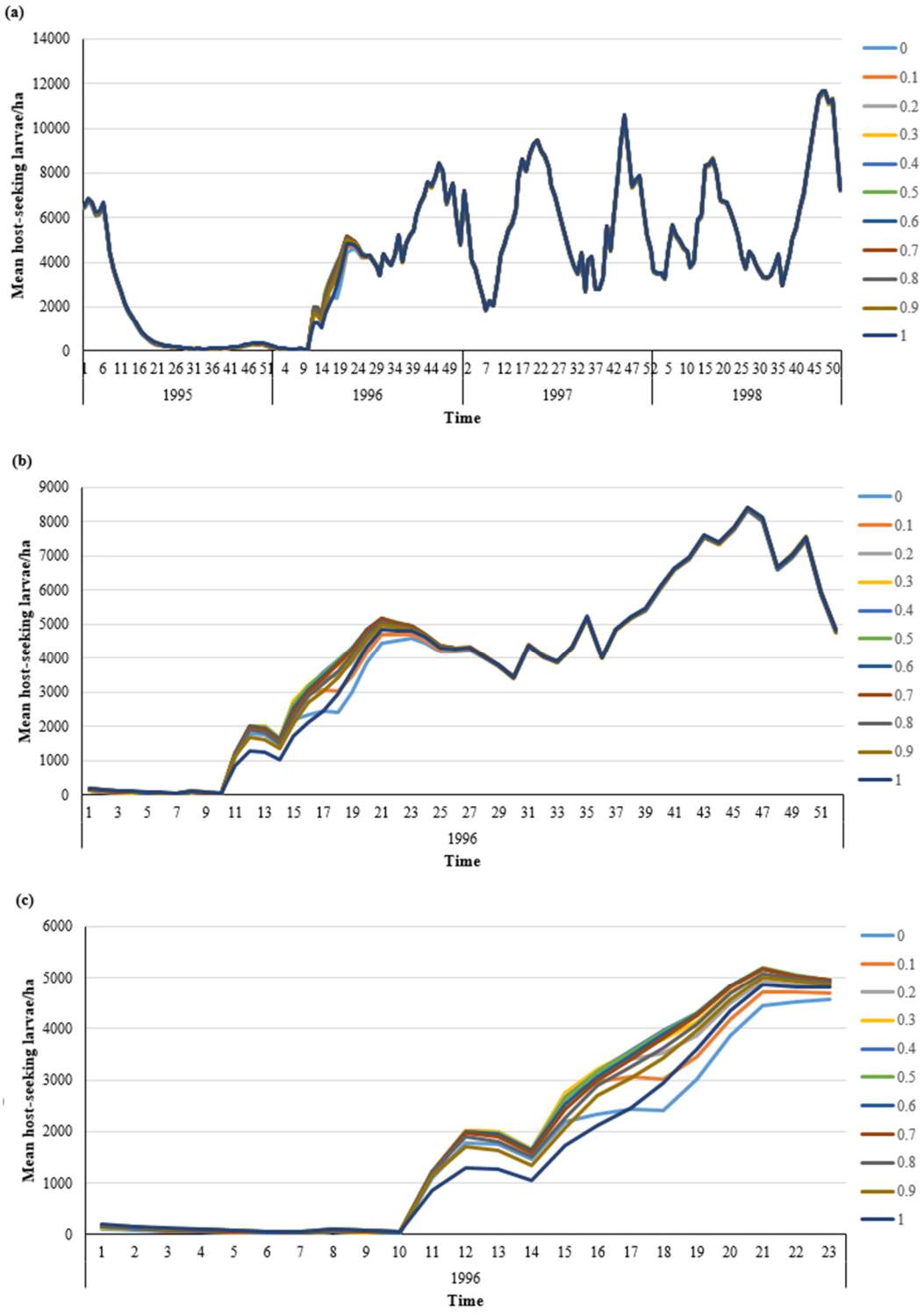

Figure 5.16. Landscape-level responses of host-seeking larvae populations of cattle-fever ticks to a 52-week pasture vacation eradication protocol initiated in January of 1995 (i.e. Cattle Off), for (a) the simulations in which both cattle and white-tailed deer (WTD) were present and where changes in WTD habitat preferences[1] (colored lines) were included. Expanded details are provided for (b) the 52-week and (c) the 23-week periods immediately following the end of the Cattle Off protocol.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

When assessing the role of WTD habitat preferences in maintaining CFT populations under different host and eradication scenarios, host-seeking larvae densities at the landscape level were very similar across the different host/eradication scenarios and habitat preferences (Figure 5.17). Densities reached their highest values (approximately 12,000 host-seeking larvae/ha) for simulations in which cattle were present (i.e., C+WTD and Cattle Off), regardless of habitat preference. Figure 5.17 shows the results at the landscape level for simulations with extremes in habitat preference values (i.e., 0.1 and 0.9 preferences for mesquite); these landscape-level patterns and magnitudes were consistent throughout all other values of habitat preferences.

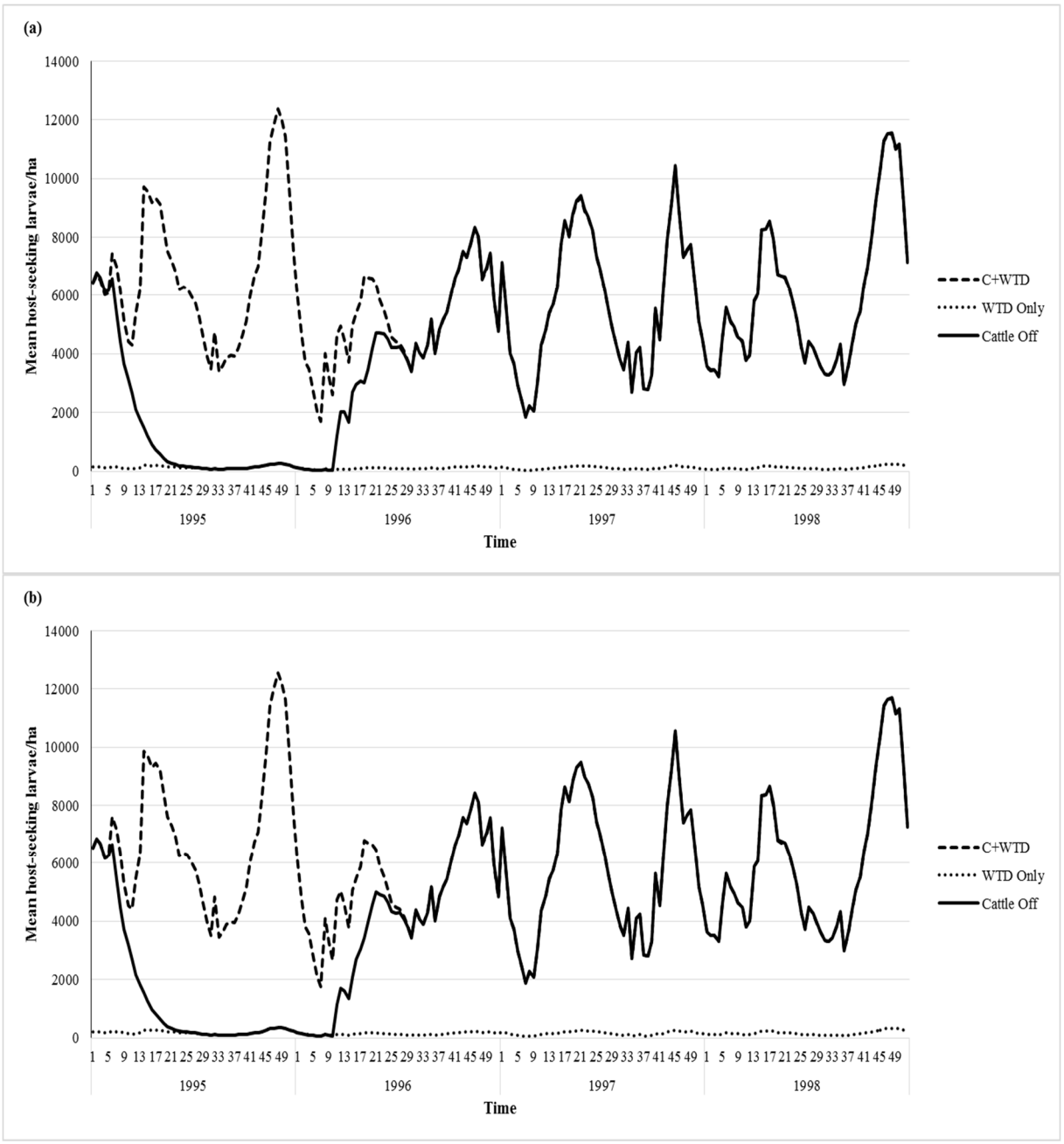

Figure 5.17. Landscape-level temporal trends in densities of host-seeking larvae populations of cattle-fever ticks for different combinations of host/eradication scenarios [1] and white-tailed deer (WTD) habitat preferences[2] during the 4-year simulation period in which WTD preference for mesquite was (a) 0.1 and (b) 0.9.

[1.] WTD Only = white-tailed deer (WTD) only; Cattle Off = 52-week pasture vacation; C+WTD = cattle and WTD.

[2.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite). Only the results of preferences 0.1 and 0.9 are shown in this figure. These patterns and magnitudes were consistent throughout all other values of habitat preferences.

To explore possible differences among habitat preferences in overall treatment efficacy, I focused on the details of the population dynamics during the recovery period using several "recovery indexes" as described in the "*Methods*" Section.

Despite differences in the response of CFT populations during the recovery period to different habitat preferences (Figure 5.16), the efficacy of the eradication protocol at the landscape level was not evident (Figure 5.17), based on the host-seeking larvae temporal trends in response to different host/eradication scenarios across different values of habitat preferences. As shown in Figure 5.17, host seeking larvae densities at the landscape level reached similar values at similar points throughout the simulation period, across different habitat preferences, regardless of host/eradication scenario.

The duration of the recovery period was imposed by climate conditions and influenced by habitat-specific survival and development rates (Figure 5.16). Pre-treatment densities of host-seeking larvae reached 8,117 larvae/ha on week 52 of the year 1994. Density of host-seeking larvae declined sharply at the start of the treatment year (week 1 of 1995) and continued decreasing until reaching a low of approximately 96 larvae/ha by week 30 of the year 1995, followed by a slight recovery in the last quarter of the year 1995, coinciding with increased precipitation and moderate temperatures during that period.

Host-seeking larvae recovery at the landscape level started during week 10 of the year 1996 and lasted until week 23 for preferences 0 and 0.1, and until week 21 for all other preferences (Figure 5.16). Towards the end of the recovery period, all densities greatly overlapped; the population of

host-seeking larvae at the landscape level reached pre-treatment levels by week 47 of 1996, and the system resumed pre-treatment dynamics within 2 years of the start of the eradication protocol. These results make sense when tick habitat quality, host-specific tick loads, and habitat preferences of cattle are taken into consideration.

Differences in the efficacy of the eradication protocol among habitat preferences at the landscape and habitat levels, based on the mean number of host-seeking larvae weeks, are presented in Figure 5.18 and Figure 5.19. Habitat preferences did have a significant effect ($p < 0.05$) on the mean host-seeking larvae weeks values at the landscape level, with higher means for habitat preferences 0 and 0.1, and lower means for habitat preferences 0.9 and 1 (Figure 5.18). These results were reasonable, considering the higher values of host-seeking larvae weeks for the eradication scenario when WTD preferences for mesquite were low, resulting in two extra weeks for the system to accumulate CFTs before reaching the recovery peak (Figure 5.16). Despite statistically significant differences, efficacy of the eradication protocol for intermediate (0.2 – 0.8) values of WTD habitat preferences was basically the same (Figure 5.18).

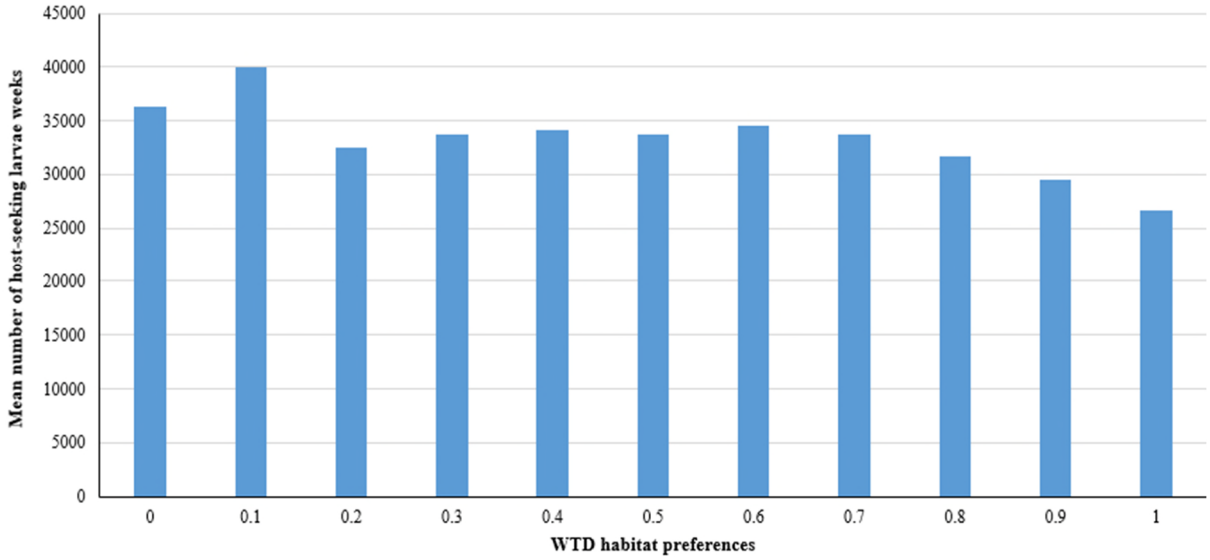

Figure 5.18. Mean number of host-seeking larvae weeks at the landscape level, by white-tailed deer habitat preference[1], during the recovery period[2] in 1996, following the end of the 52-week Cattle Off pasture vacation protocol implemented for cattle-fever tick eradication in 1995.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

[2.] Weeks 10 – 23 of 1996 for habitat preferences 0 and 0.1; weeks 10 – 21 of 1996 for all other habitat preferences.

At the habitat level, the effect of habitat preferences on mean host-seeking larvae weeks was significant ($p < 0.05$), with mixed-brush having much lower values compared to mesquite and uncanopied grass (Figure 5.19). Similarly, the interaction between habitat preferences and habitat type had a statistically significant effect ($p < 0.05$) on host-seeking larvae weeks, with lower preferences for mesquite (i.e., 0 and 0.1) having the highest mean host-seeking larvae week values across habitat types. As shown in Figure 5.19, the habitat types most preferred by cattle (i.e., uncanopied grass and mesquite) had values of host-seeking larvae weeks similar to those observed at the landscape level (Figure 5.18).

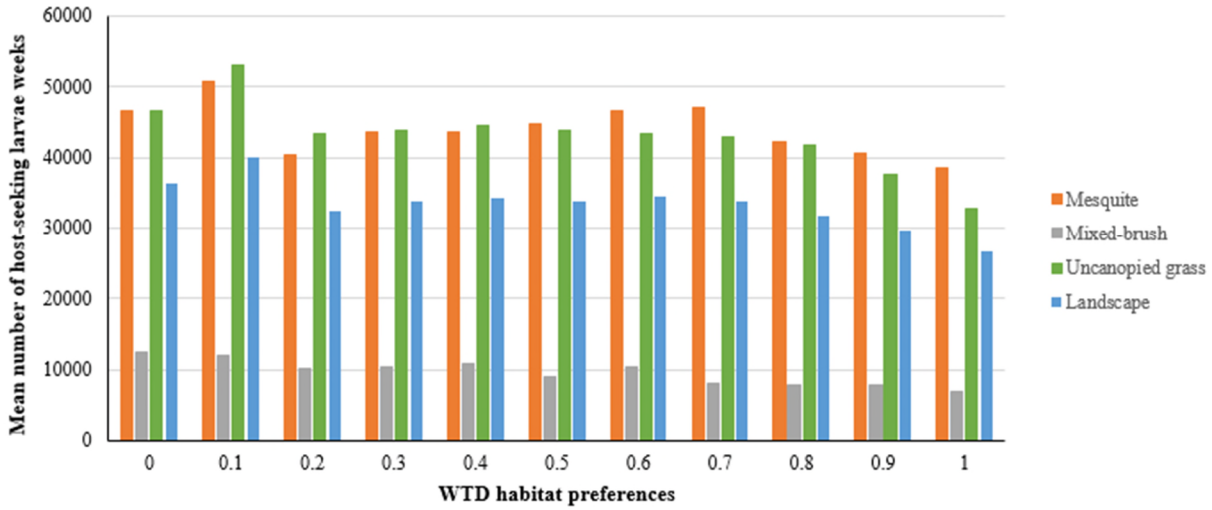

Figure 5.19. Mean number of host-seeking larvae weeks at the landscape level and by habitat type, across white-tailed deer (WTD) habitat preferences[1], during the recovery period[2] in 1996, following the end of the 52-week Cattle Off pasture vacation protocol implemented for cattle-fever tick eradication in 1995.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

[2.] Weeks 10 – 23 of 1996 for habitat preferences 0 and 0.1; weeks 10 – 21 of 1996 for all other habitat preferences.

When considering host-seeking larvae densities at the beginning of the recovery period (Figure 5.20), the landscape-level values fell between the maximum and the minimum values at the habitat level. The mean number of host-seeking larvae in uncanopied grass was the lowest, and as WTD preference for mesquite increased, densities of host-seeking larvae at the start of the recovery period decreased in mixed brush and increased in mesquite.

When considering host-seeking larvae densities at the end of the recovery period (i.e., the maximum number of host-seeking larvae at weeks 21 – 23, depending on habitat preferences), the effect of WTD habitat preferences on host-seeking larvae densities was less evident at the individual habitat level and even less at the landscape level (Figure 5.21).

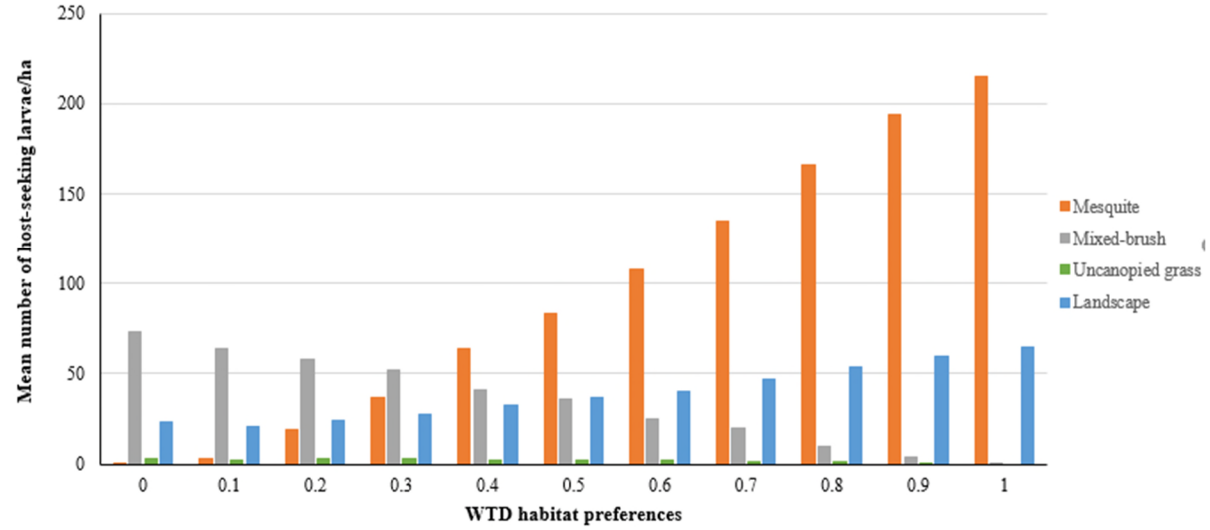

Figure 5.20. Mean number of host-seeking larvae, at the landscape level and by habitat type, across white-tailed deer (WTD) habitat preferences[1], at the beginning of the recovery period[2] following the end of the 52-week Cattle Off pasture vacation protocol implemented for cattle-fever tick eradication in 1995.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

[2.] Week 10 of 1996 for all habitat preferences.

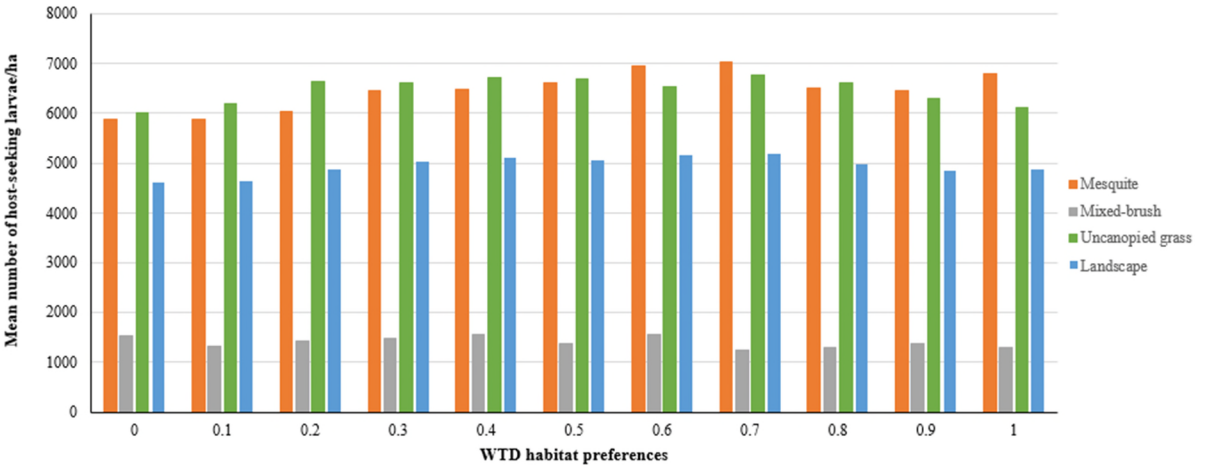

Figure 5.21. Mean number of host-seeking larvae, at the landscape level and by habitat type, across white-tailed deer (WTD) habitat preferences[1], at the end of the recovery period[2] following the end of the 52-week Cattle Off pasture vacation protocol implemented for cattle-fever tick eradication in 1995.

[1.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

[2.] Weeks 10 – 23 of 1996 for habitat preferences 0 and 0.1; weeks 10 – 21 of 1996 for all other habitat preferences.

When considering individual habitat types, the dynamics of host-seeking larvae in uncanopied grass for different values of habitat preference (Figure 5.22 and Figure 5.23) closely resembled those observed at the landscape level (Figure 5.17). However, the response of the simulated CFT population to different combinations of hosts and habitat preferences showed interesting differences in both patterns and magnitudes (Figure 5.22 and Figure 5.23), within the mesquite and mixed-brush habitats. The particulars of these responses are presented in the sections below.

5.3.1 Mesquite

For the Cattle Off simulations, when WTD habitat preferences for mesquite were low (i.e., preference = 0.1), tick populations within mesquite were largely suppressed, reaching values of less than 4 host-seeking larvae/ha (less than 0.1% of the pre-treatment density) during week 10 of 1996 and recovering to a density of approximately 5,975 host-seeking larvae/ha (approximately 62% of the pre-treatment level) during week 23 of 1996 (Figure 5.22). By week 27 of 1996, densities of host seeking larvae for both simulations in which cattle were present (i.e., C+WTD and Cattle Off) were similar, and temporal patterns of host-seeking larvae populations largely overlapped within the mesquite habitat from that point on.

For the Cattle Off simulations, when WTD habitat preferences for mesquite were high (i.e., preference = 0.9), tick populations within the mesquite habitat reached a low of approximately 192 host-seeking larvae/ha (from a starting density of approximately 9,982) and recovered to a density of approximately 6,811 host-seeking larvae/ha (approximately 68% of the pre-treatment population) by week 21 of 1996 (Figure 5.23). Under this high preference value, the host-seeking larvae population within mesquite habitat showed a slight increase during week 48 of 1995; this corresponded to a period of increased precipitation and warmer winter temperatures, which

coupled with the habitat suitability and preference value, made sense in terms of a population recovery within mesquite.

For WTD Only simulations, densities of host-seeking larvae within mesquite habitats were relatively low across all values of habitat preferences, fluctuating between approximately 30 – 110 host-seeking larvae/ha for simulations in which habitat preference was 0.1 (Figure 5.22), and between approximately 180 – 1,067 host-seeking larvae/ha for simulations in which habitat preference was 0.9 (Figure 5.23).

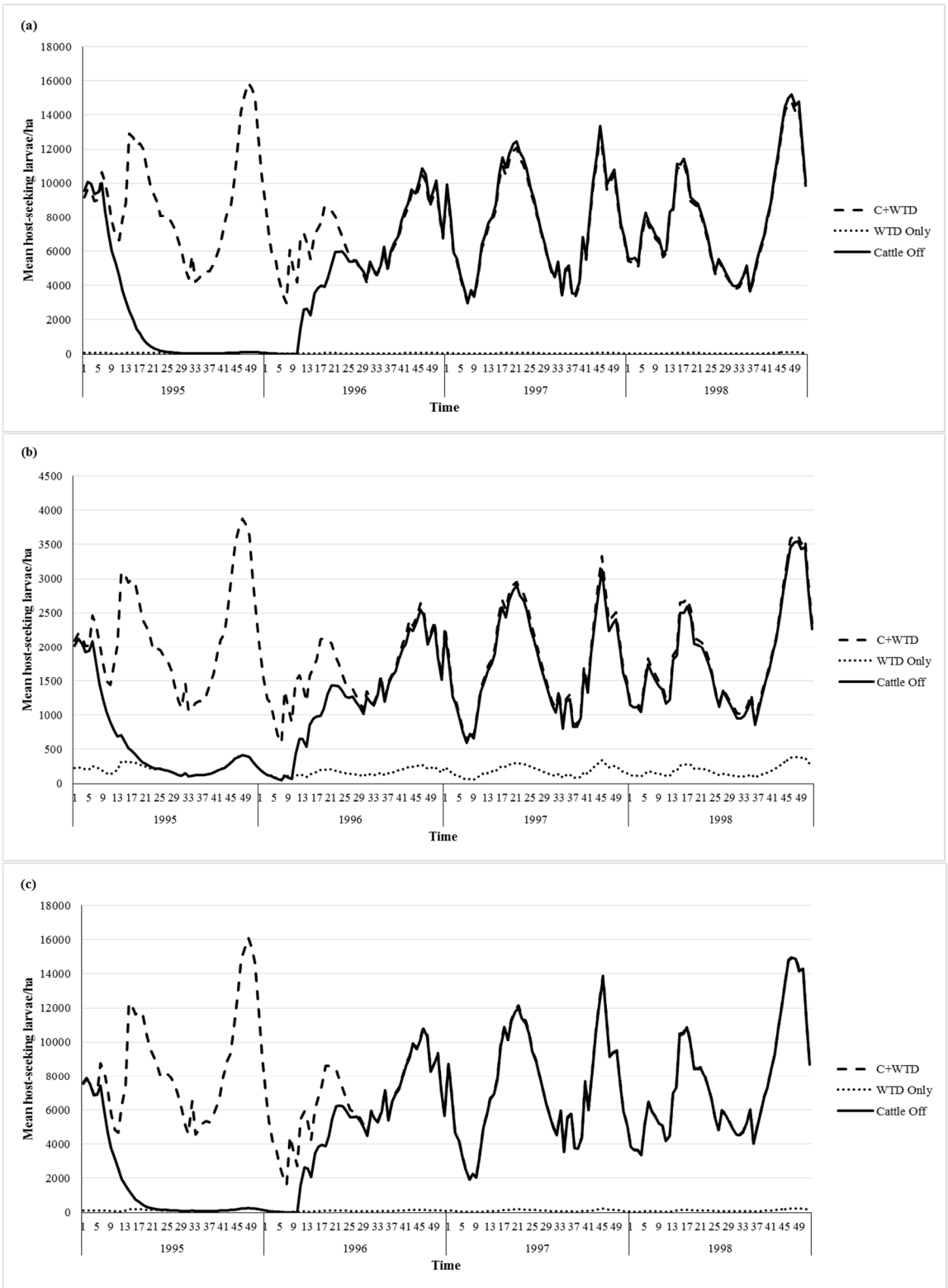

Figure 5.22. Habitat-level temporal trends in densities of host-seeking larvae populations of cattle-fever ticks on (a) mesquite, (b) mixed brush, and (c) uncanopied grass, during simulations with different host/eradication scenarios[1] and in which WTD habitat preference for mesquite was 0.1.

[1.] WTD Only = white-tailed deer (WTD) only; Cattle Off = 52-week pasture vacation in the year 1995; C+WTD = cattle and WTD.

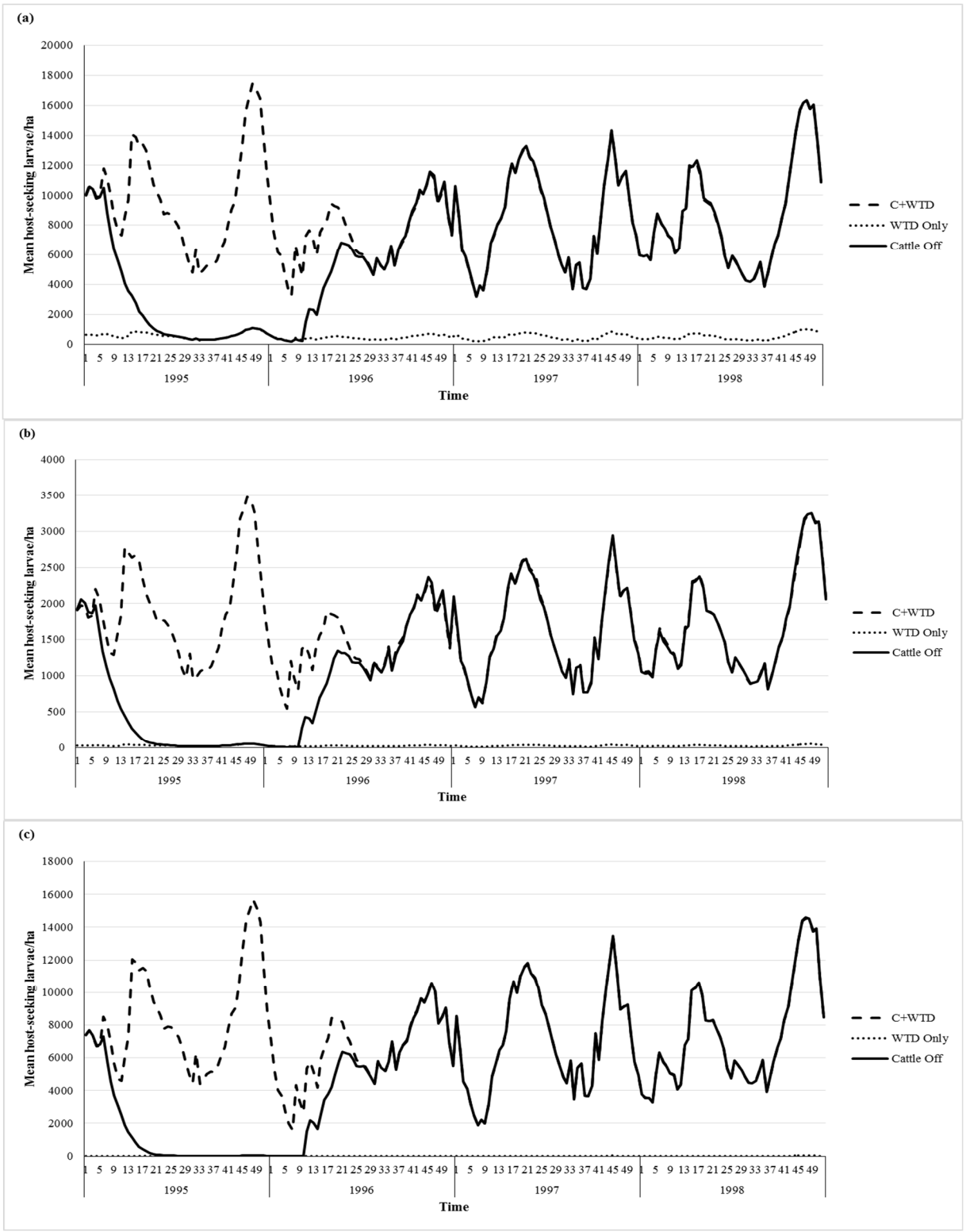

Figure 5.23. Habitat-level temporal trends in densities of host-seeking larvae on (a) mesquite, (b) mixed brush, and (c) uncanopied grass, during simulations with different host/eradication scenarios[1] and in which WTD habitat preference for mesquite was 0.9.

[1.] WTD Only = white-tailed deer (WTD) only; Cattle Off = 52-week pasture vacation in the year 1995; C+WTD = cattle and WTD.

5.3.2 Mixed-brush

For the Cattle Off simulations, when WTD habitat preferences for mesquite were low (i.e., preference = 0.1), corresponding to high preferences for the other two habitat types, host-seeking larvae populations within mixed-brush were reduced to approximately 50 host-seeking larvae/ha (approximately 2% of the pre-treatment density levels), recovering to approximately 1,434 host-seeking larvae/ha (approximately 71% of the pre-treatment density) by week 23 of 1996 (Figure 5.22). By week 33 of 1996, densities of host seeking larvae within mixed-brush were similar between both simulations in which cattle were present (i.e., C+WTD and Cattle Off), and temporal patterns of host-seeking larvae populations largely overlapped within this habitat type from that point on.

For the Cattle Off simulations in which WTD habitat preferences for mesquite were high (i.e., preference = 0.9), corresponding to low preferences for the other two habitat types, CFT populations within the mixed-brush reached a low of approximately 4 host-seeking larvae/ha (approximately 0.2% of the pre-treatment density), recovering to approximately 1,347 host-seeking larvae/ha (approximately 70% of the pre-treatment level) by week 21 of 1996 (Figure 5.23).

For all of the Cattle Off simulations, host-seeking larvae temporal trends within mixed-brush showed a short-term increase during week 48 of 1995, regardless of habitat preference value (Figure 5.22 and Figure 5.23), which corresponded with the favorable climate conditions for survival of host-seeking larvae. The magnitude of this short-term increase in densities depended on the habitat preference value, being more evident as preference for mesquite decreased; however,

host-seeking larvae densities in mixed-brush did not fall below 4 host-seeking larvae/ha, under any combination of hosts, even under low preferences for this habitat type.

For the WTD Only simulations, densities of host-seeking larvae within mixed-brush were relatively low across all values of habitat preferences, fluctuating between approximately 280 – 2,037 host-seeking larvae/ha for simulations in which preference for mesquite was 0.1 (i.e., high preference for mixed-brush; Figure 5.22), and between approximately 40 – 231 host-seeking larvae/ha for simulations in which habitat preference for mesquite was 0.9 (i.e., low preference for mixed-brush; Figure 5.23).

5.3.3 Uncanopied Grass

Within the uncanopied grass habitat, the response of host-seeking larvae populations to different host/eradication scenarios was very similar across WTD habitat preferences (Figure 5.22 and Figure 5.23). Host-seeking larvae densities in uncanopied grass were the highest when both cattle and WTD were present, reaching densities higher than in any other habitat type (above 16,102 host-seeking larvae/ha), regardless of habitat preference value (Figure 5.22 and Figure 5.23), and reaching their lowest value when cattle vacated the pasture, independent of the habitat preference.

When cattle vacated the pasture, the host-seeking larvae population within uncanopied grass was largely suppressed across all habitat preference values, reaching densities as low as 0.6 host-seeking larvae/ha during week 10 of 1996 (Figure 5.23). However, the CFT population recovered quickly, and by week 21 of 1996, it reached densities of approximately 6,364 host-seeking larvae/ha (approximately 85% of the pre-treatment level).

As expected, the densities of host-seeking larvae in uncanopied grass decreased as WTD habitat preference for mesquite increased, regardless of the particular combination of hosts. For WTD Only simulations, the temporal patterns of CFT populations were similar to those observed across the different values of habitat preferences for the C+WTD scenario (Figure 5.22 and Figure 5.23). However, the densities of host-seeking larvae within uncanopied grass throughout the 4-year simulation period were much lower for WTD Only simulations (between approximately 18 – 238 host seeking larvae/ha for preference 0.1 and approximately 2 – 26 for preference 0.9) compared to C+WTD simulations (between approximately 1,619 – 16,102 for preference 0.1 and 1,587 – 15,677 for preference 0.9).

For a more detailed analysis of the system, I selected the peak of maximum host-seeking larvae density towards the end of the 4-year simulation (week 48 of year 1998) to explore the effect of habitat preferences on the efficacy of the eradication protocol. When focusing on a specific point in time, differences in mean host-seeking larvae densities at the landscape level among habitat preferences within each host/eradication scenario were statistically significant ($p < 0.05$). However, the magnitude of these changes in host-seeking larvae densities among the different host/eradication scenarios across different values of habitat preference was relatively small.

Host-seeking larvae densities ranged from 11,523 – 11,664 host-seeking larvae/ha in the C+WTD scenario; from 231 – 335 host-seeking larvae/ha in the WTD Only scenario; and from 11,559 – 11,700 in the Cattle Off scenario. Furthermore, despite the statistical significance, relative relationships among the different host/eradication scenarios were unaffected by changes in habitat

preferences (Figure 5.24), with WTD Only simulations having consistently the lowest mean host-seeking larvae densities at the landscape level for all habitat preferences.

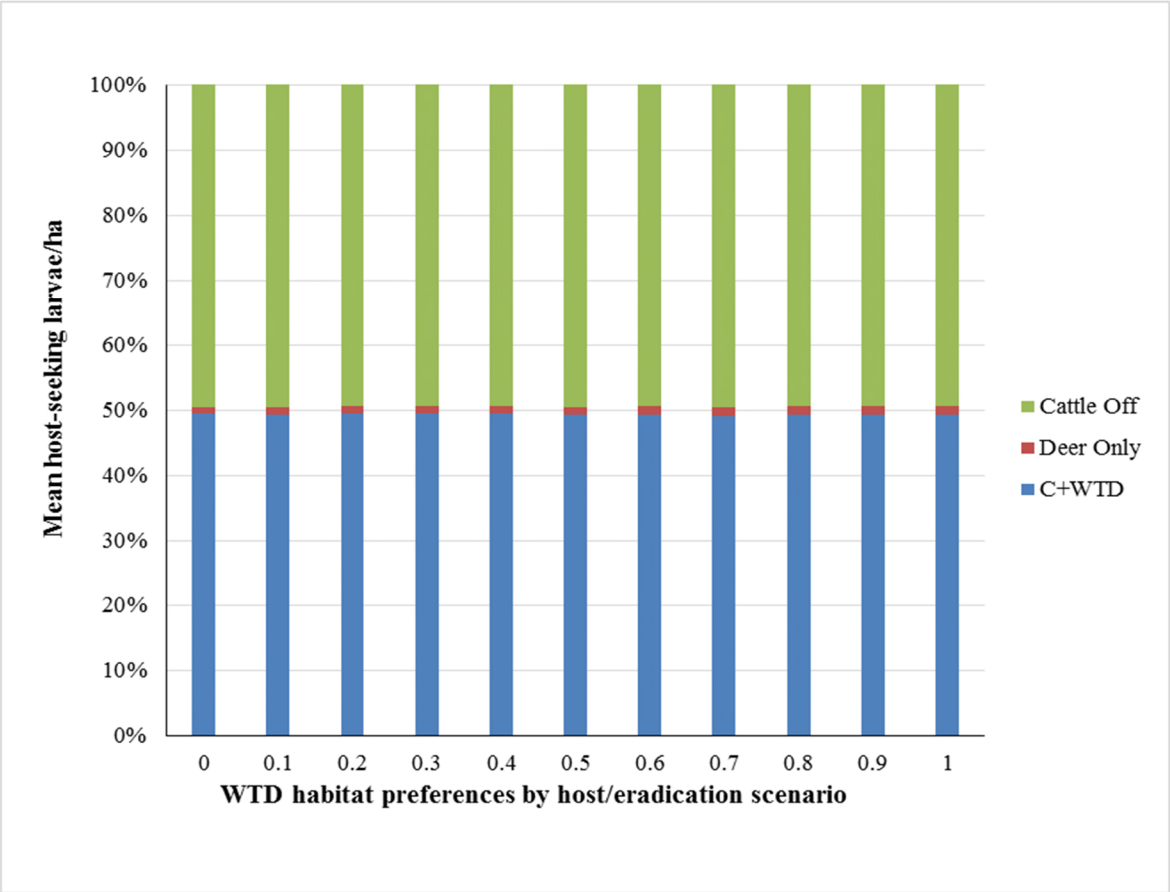

Figure 5.24. Relative mean host-seeking larvae densities at the landscape level by host/eradication scenario[1] across white-tailed deer habitat preferences[2], during the peak density week (week 48 of 1998) selected towards the end of the 4-year simulation.

[1.] WTD Only = white-tailed deer (WTD) only; Cattle Off = 52-week pasture vacation in the year 1995; C+WTD = cattle and WTD.

[2.] Habitat preferences varied from 0 (no preference for mesquite) to 1 (complete preference for mesquite).

When examining the effect of habitat preferences on the efficacy of the eradication protocol among habitat types, quantitative and relative differences in the mean number of host-seeking larvae across the different host/eradication scenarios were observed (Figure 5.25 and Figure 5.26).

Regardless of the particular combination of hosts and habitat preferences, host-seeking larvae densities reached higher levels in mesquite compared to other habitat types (Figure 5.25).

As shown in Figure 5.26, when WTD were the only host present, densities of host-seeking larvae during the week of peak density towards the end of the 4-year simulation (week 48 of 1998) were relatively high within mixed-brush, even under high preference of WTD for mesquite (preferences of 0.8 and 0.9). Conversely, host-seeking larvae densities in uncanopied grass decreased as habitat preference for mesquite increased.

The effect of habitat preferences and host/eradication scenario on the mean number of host-seeking larvae changed among habitat types during the week of peak density. In mesquite and mixed-brush, both habitat preference and host/eradication scenario had a significant effect ($p < 0.05$) on host-seeking larvae densities; on the other hand, habitat preferences did not have a significant effect ($p > 0.05$) on host-seeking larvae densities in uncanopied grass, but the effect of the different host/eradication scenarios was significant.

Despite the statistically significant differences, relative relationships among different host/eradication scenarios were unaffected by habitat type, with mixed-brush and uncanopied grass consistently supporting the lowest and the highest mean host-seeking larvae densities, respectively, for all host/eradication scenarios across habitat preferences.

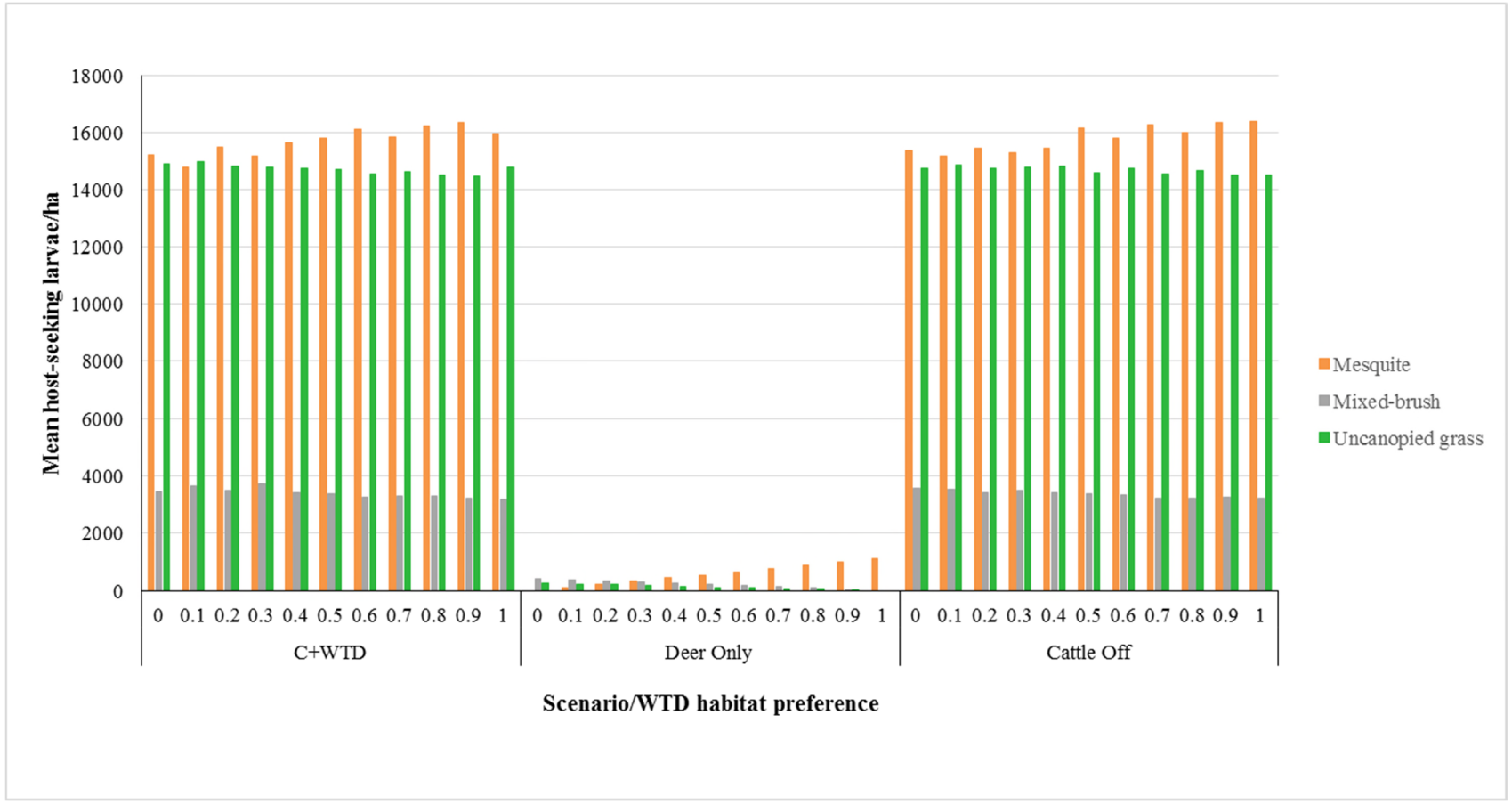

Figure 5.25. Mean host-seeking larvae densities across host/eradication scenarios and white-tailed deer (WTD) habitat preferences, at the landscape level and habitat level, during the peak density week (week 48 of 1998) selected towards the end of the 4-year simulation.

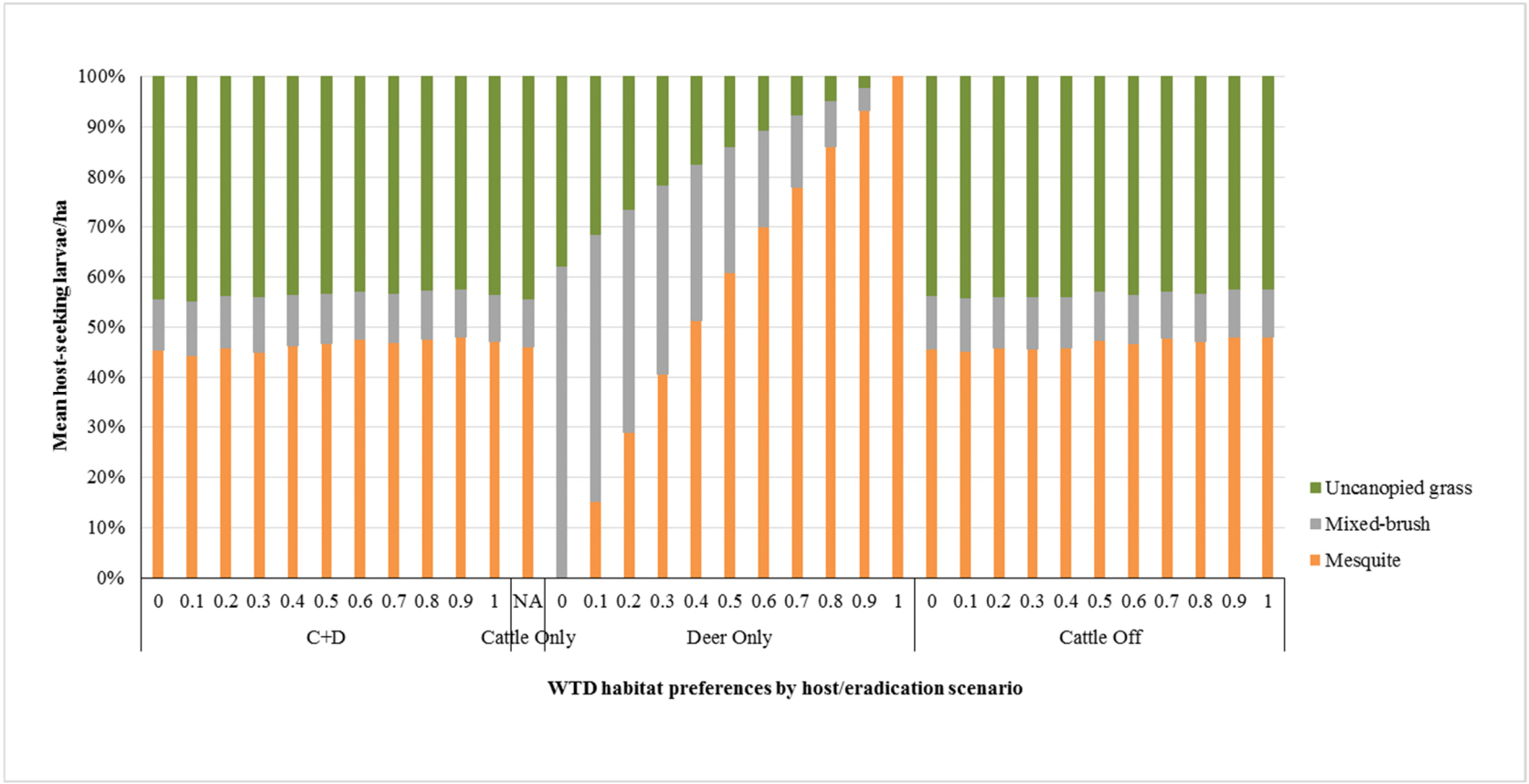

Figure 5.26. Relative mean density of host-seeking larvae by host/eradication scenario and habitat type across habitat preferences during the peak density week (week 48 of 1998) selected towards the end of the 4-year simulation.

6 DISCUSSION

Species-specific behavior has been proposed as one of the areas where more research is needed in understanding the effectiveness of disease management strategies in the wildlife-livestock interface (Foley et al. 2017). The model presented here is the first attempt to address a knowledge gap in how the interaction between behavioral traits of individual ungulate hosts and habitat-level characteristics affect the population dynamics of CFT, with implications for eradication and control strategies.

Use of space and habitat preferences of WTD, although widely studied (Sanders 1963, Inglis et al. 1979, Beier and McCullough 1990, Coe et al. 2004, Depew 2004, Brunjes et al. 2006), are poorly understood in the context of CFT management strategies in multi-host systems. Similarly, although several studies have examined the influence of climate and habitat on the population dynamics of CFT (Teel et al. 1996, Estrada-Peña et al. 2006b) they have not considered the role of behavioral traits of ungulate hosts within the context of the tick-habitat-host relationships.

Other studies have examined movement patterns of ungulate hosts in the context of disease transmission (Clements et al. 2011), the efficacy of targeting acaricides at specific types of hosts (Wang et al. 2012), the effect of seasonal fluctuations in host communities on the dynamics of infectious disease (Wang et al. 2015), and the effect of changes in host diversity and community composition on disease risk (Schmidt and Ostfeld 2001). None of these studies have been applied within the context of the effect of habitat preferences of ungulate hosts on CFT populations. The model of Wang et al. (2016), from which my model draws, was

the first attempt to address how the interactions of climate variation and ungulate hosts (specifically cattle and WTD) impact CFT eradication efforts.

As expected, model estimates of CFT densities fluctuated through time as a response to climate variables, environmental conditions, and availability of hosts known to affect growth, survival and development of ticks (Mount et al. 1991, Ogden et al. 2005, Estrada-Peña and Salman 2013). These results are in agreement with studies on CFT populations in South Texas conducted by Teel et al. (1996), Corson et al. (2004), and Wang et al. (2012, 2015). The magnitude of these responses differed among and within years, as a response to intra- and inter-annual variation in climate conditions, and among life stages, with climate variables having a disproportionate effect on off-host ticks (i.e., host-seeking larvae and engorged adults) compared to on-host adult ticks.

As expected, environmental conditions influenced tick population dynamics differently across life stages, reflecting their influence on oviposition rates, egg incubation periods, development rates, and host-seeking activity (Teel 1984, Needham and Teel 1991, Estrada-Peña 1999, Estrada-Peña et al. 2006a). Densities of adult ticks on cattle and WTD responded little to temporal changes in climate variables, except for the decreases in infestation evidenced during the winter months. This decrease corresponded to a period when low temperatures affected survival, development, and activity rates of the various life stages of CFT (Corson et al. 2004, Leal et al. 2018, McClure and Diuk-Wasser 2019).

Climate conditions, on the other hand, had a stronger effect on off-host life stages, being more pronounced on the temporal responses of host-seeking larvae compared to engorged adults. Host-

seeking larvae was the life stage where the response of CFT populations to climate variables and the different combinations of hosts were more evident. CFT spend the majority (up to 90%) of the life cycle as host-seeking larvae (Needham and Teel 1991); therefore, environmental conditions could have a disproportionate effect on this life stage, as they can live 4 – 6 months (or more, depending on environmental conditions) waiting for a host (Leal et al. 2018). The number of engorged adults dropped from each host into the landscape changed less as a response to environmental conditions, as expected due to their short lifespans (Haytham et al. 2018), suggesting that the influence of environmental conditions on survival of engorged adults would have to be very strong to be noticeable.

Changes in habitat preferences did not have a visible effect on the densities of engorged adults or host-seeking larvae at the landscape level for simulations where both cattle and WTD were present. At the habitat level, however, changes in tick density as a response to WTD habitat preferences were evidenced, at least within some habitat types. The magnitude of these differences varied depending on the particular combination of host/eradication scenarios (i.e., WTD Only, C+WTD, and Cattle Off) and habitats. This result suggests that WTD drive tick populations in the habitats least preferred by cattle, and that the role of WTD in the dynamics of CFT populations is enhanced by the effect of habitat suitability for tick survival and development.

While climate variables influence tick phenology due to temperature and relative humidity thresholds below which survival and development of ticks is inhibited (Davey et al. 1991), the effect of environmental conditions can be confounded by availability and abundance of hosts (Wang et al. 2015) and by landscape heterogeneity and habitat configuration (Teel 1991, Estrada-

Peña and Venzal 2006). Use of space by WTD is influenced by the distribution of resources across the landscape at different spatial and temporal scales (Webb et al. 2007, Clements et al. 2011); this spatial-temporal mediated utilization of resources results in areas of concentrated use within their home ranges, with implication for their role in the maintenance of CFT populations. My results of CFT densities at the landscape and habitat levels suggested that in the presence of cattle, the role of WTD could be underestimated, highlighting the importance of spatial scales.

For simulations in which both hosts were present, uncanopied grass and mesquite were the habitats that consistently supported the highest densities of host-seeking larvae, but were also the habitat types where differences in host-seeking larvae densities were less evident. Uncanopied grass was the habitat more preferred by cattle (preference 0.6) but also the poor quality habitat in terms of tick survival; mesquite was the good habitat in terms of suitability for CFT, but it was not as preferred by cattle (preference 0.3). This suggests that cattle preferences for specific habitat types play an important role in shaping the particular interactions between habitat suitability and tick development and survival, maintaining CFT populations at the landscape level through their effect at the habitat level.

Despite consistently supporting the lowest densities of host-seeking larvae, mixed-brush was the habitat type where the largest differences in host seeking larvae were observed, regardless of habitat preference. The magnitude of these differences changed based on the particular interactions with WTD habitat preferences for mixed-brush and habitat quality, relative to the survival and development of ticks, suggesting that the role of WTD in maintaining CFT populations is habitat-dependent.

The system was dominated by cattle and the effect of WTD habitat preferences on host-seeking larvae densities was largely determined by the presence (or absence) of cattle. When cattle were absent, the influence of WTD on CFT population dynamics was evident both at the landscape and habitat level. When cattle were present, the role of WTD was not evident at the landscape level; however, the dynamics of CFT populations within those habitats less preferred by cattle were determined by changes in WTD preferences, highlighting the importance of spatial scales and species-specific habitat preferences in the context of CFT infestations and eradication strategies.

The role of WTD in maintaining populations of CFT has been the focus of many studies, with mixed results. Davey (1990) found that *Boophilus* sp ticks reared on WTD could not be sustained through successive generations, while studies conducted by Park et al. (1966) and Gray et al. (1979) have found that these ticks were capable of completing repeated life cycles on WTD. Results from my study indicated that infestations of CFT on WTD were maintained throughout the simulation period, even during the pasture vacation eradication scenario, supporting the idea that WTD appear to sustain CFT populations in the absence of cattle over long periods of time (Pound et al. 2010).

Habitat-level differences in the response of CFT populations to the host/eradication scenarios simulated in this study suggest the existence of a spatial scale component in the effect of WTD habitat preferences on the effectiveness of eradication strategies. Mixed-brush was the habitat type with the highest densities of host-seeking larvae at the beginning of the recovery period, and densities of host-seeking larvae did not fall below a threshold number across all values of habitat

preferences, indicating that even when preference for mixed-brush was very low, this habitat played an important role in sustaining CFT populations. These results support the idea that wildlife might be a complicating factor in the eradication of CFT (George 1990, Pérez de León et al. 2012).

CFT population responses to all the simulated combinations of hosts and habitat preferences were consistent with historic records of infestations summarized by Pound et al. (2010), and with studies showing low-level, continuous infestations sustained by WTD in South Texas (Currie 2013). The response of CFT populations to the pasture vacation scenario was limited to the particular climate profile of the year 1995, the year selected for pasture vacation in this study. Differences in treatment efficacy related to inter-annual variation in climate conditions were not taken into account; therefore, a pasture vacation in other years might have yielded different results, as shown by Wang et al. (2016), who reported statistically significant differences in overall treatment efficacy within each of the eradication scenarios considered, among weather profiles.

The results from the different host/eradication scenarios indicated that densities of CFT at the landscape level seemed to be more susceptible to the presence (or absence) of cattle than to changes in WTD habitat preferences; conversely, differences at the habitat level seemed to be influenced by changes in habitat preferences and habitat suitability for CFT. Densities of CFT in uncanopied grass, the preferred habitat by cattle, did not seem as influenced by WTD habitat preferences as by the host/eradication scenario, while densities of CFT in mixed-brush, the habitat least preferred by cattle, seemed to be influenced by changes in habitat preference. This suggests that habitat preferences and their interaction with tick habitat suitability play an important role in the

maintenance of tick populations, supporting the idea that differences at the habitat level do not necessarily correspond with patterns observed at the landscape level.

CFT temporal trends in densities at the landscape level were very similar across habitat preferences; this result was unexpected given the different host and eradication scenarios considered in this study. After a closer inspection of the system at the habitat level, finer-scale differences emerged, suggesting that the role of WTD in maintaining CFT populations has a spatial component that shapes the particular interaction between habitat preference and habitat suitability for CFT.

When considering individual habitat types, the dynamics of host-seeking larvae during the recovery period showed interesting differences both in patterns and in magnitudes, with the response to each combination of hosts being dependent upon the particulars of the habitat preference-habitat type interaction. These results support the idea that in the presence of cattle, the role of WTD in maintaining populations of CFT can be overlooked, and suggest that habitat type characteristics are a necessary consideration when investigating the influence of habitat preference of hosts on the efficacy of eradication strategies.

There are some considerations when interpreting the results of this study. First, these results are based on one simulation model representing the dynamics of CFT populations using one of the many available modelling approaches reviewed by Wang et al (2017). Second, the application of this model to assess the effectiveness of the pasture vacation protocol as a measure for CFT eradication was limited to the particulars of host and environmental conditions of South Texas

rangelands (Wang et al. 2016). Third, although habitat preferences change through time as a response to changes in biotic and abiotic factors (Bello et al. 2001, Matthiopoulos 2003), they were held constant throughout each simulation period. Fourth, parametrization of the model had implicit the disproportionate effect of cattle on CFT populations because cattle carried 10 times as many ticks as WTD (Wang et al. 2016).

These assumptions and choices in model development and parametrization, however, were justified. First, I chose a validated model that produced acceptable estimates of fluctuations in CFT densities as the base for my model (Wang et al. 2016). Second, these results represent the response of CFT populations to a wide range of environmental variables across a wide geographic range; therefore, they can aid in the understanding of the general relationship between host habitat usage, tick densities, and tick-borne pathogens (Estrada-Peña et al. 2008). Third, methods for the analysis of resource use and selection range from the simple correlational (Thomas and Taylor 2006) to the more sophisticated, predictive approaches, that explicitly incorporate landscape structure and function into the study of resource selection and habitat use (Manly et al. 2002, Marzluff et al. 2004). Fourth, although the relative differences in CFT burdens were a result of model parametrization, the trends and relationships in the absolute values of spatial and temporal tick densities emerged as system-level properties (Wang et al. 2016).

The impacts of global change on CFT can be explored by simulation models that include climate-space-host interactions, through the identification of specific cause-effect relationships capable of generating observed patterns of recurring CFT infestations and re-emerging tick-borne diseases. Models like the one presented in this study, aiming at gaining a better understanding of how animal

behavior and abiotic factors interact at different temporal and spatial scales, can be applied to the understanding of how these patterns and processes might be altered by specific management strategies, providing a useful tool for the identification of effective eradication strategies.

The threat of CFT introduction into Texas rangelands is increased by the evolution of resistance to acaricides (Abbas et al. 2014) and the ability of CFT to utilize native and exotic ungulates as alternate hosts (Pound et al. 2010). Several ungulate species that coexist in Texas rangelands, including WTD, Nilgai antelope, and wild boar, have been implicated in the maintenance of CFT populations, through their role as suitable hosts (Kistener and Hayes 1970, Cooksey et al. 1989, Corn et al. 2016), and/or by dispersing ticks throughout the landscape (Gray et al. 1979, Foley et al. 2017). These interactions tick-host-landscape have implications for infestation and re-infestation of CFT inside, and potentially outside, of quarantine zones (Graham and Hourrigan 1977, Busch et al. 2014, Lohmeyer et al. 2018).

Spatial changes in environmental variables across the landscape can interact with the physiological traits of off-host parasitic arthropods to shape their distribution (Estrada-Peña et al. 2016). Landscape-level responses in CFT densities were dominated by the presence of cattle in the system; however, changes in WTD habitat preferences seemed to play an important role at the habitat level, especially within the habitat types least preferred by cattle, suggesting that particular habitats could act as “refugia”.

Several factors have been identified as drivers of the emergence of tick-borne diseases, including climate variability, land cover change, and habitat fragmentation (Brownstein et al.

2005, Estrada-Peña and Salman 2013, Ogden et al. 2013). Habitat- and climate-mediated effects can affect the tick-host-landscape interface by causing shifts in ecological attributes such as distribution ranges and host availability (Pérez de León et al. 2012, Estrada-Peña et al. 2015).

Environmental instability has been suggested as one of the factors facilitating spatial and temporal refugia (Lorenzen et al. 2012, Sands et al. 2017). The potential effects of climate change warrant further study focused on the role of predicted refugia in shaping CFT populations to inform management strategies that could prevent introduction and establishment of CFT into new areas. Exploring the spatial relationship between distribution of CFT and habitat use by ungulate hosts could provide additional information regarding potential refugia-generating responses.

My results indicated that in the absence of cattle, CFT populations at the landscape and habitat level were maintained by WTD. A slight recovery in host-seeking larvae densities toward the end of the pasture vacation period was observed within mixed-brush; the magnitude of this increase changed across values of WTD habitat preferences, but was evident even for simulations where habitat preference for this habitat type was low. Furthermore, the minimum tick densities within this habitat type were higher than the minimum densities within mesquite and uncanopied grass, regardless of habitat preference.

Through genetic analyses, Bush et al. (2014) found evidence of local and regional persistence mechanisms for CFT infestations in Texas. Wang et al. (2016) found that WTD participated in

creating tick refugia by dispersing CFT among habitats favorable for the survival and development of off-host life stages. The results of my study indicated that the effect of WTD habitat preferences on CFT populations plays a role in maintaining CFT populations in mixed-brush, suggesting that this habitat type acts as refugia for CFT, complicating the application of eradication strategies.

Habitat suitability has been suggested as a good estimator of the life cycle of CFT (Estrada-Peña et al. 2006b); in this study, changes in WTD habitat preferences focused on preference for mesquite, the most suitable habitat for tick survival and development, based on the assumption that preference for this habitat type would have a disproportionate effect on CFT densities. My results, however, suggest that changes in WTD preference for mixed-brush might play a more important role in maintaining CFT populations, through a refugia effect mediated by the hosts' habitat preferences. Future studies exploring the relationship between habitat preferences and efficacy of control measures could focus on WTD preferences for mixed-brush. Additionally, exploring changes in habitat preference by cattle at finer spatial scales could provide additional information on the efficacy of eradication strategies.

Several of the ecological complexities related to gender-specific movement patterns by WTD (Karns et al. 2011), seasonal variation in the use of space (Cooper et al. 2008), and the presence of additional alternate hosts (Cárdenas-Canales et al. 2011), that complicate the tick-host-habitat interaction, were not considered in my model. These factors could be the focus of future investigation. Additionally, WTD density used for my simulations (0.6175 individuals per hectare; Wang et al. 2016) was in the upper end of densities reported for Texas (0.705 WTD per hectare in the Llano-Mason area; Leschper 2018), a much higher density than that estimated for South Texas

(0.0574 WTD per hectare, as of 2017; The Cattleman Magazine 2017). At such high densities, the role of WTD in maintaining CFT populations could have been overestimated.

Infestations that persist or re-emerge following eradication efforts suggest that tick-host-habitat interactions with climate and landscape may be responsible for sustaining tick populations (Pound et al 2010). Failure in the development or implementation of management strategies (Pérez de León et al. 2012), widespread or uncontrolled movements of hosts and abundance of domestic and wild animals (Clements et al. 2011, Currie 2013), and absence of an adequate understanding of the ecological plasticity of ticks (Estrada-Peña and Salman 2013) highlight the complexity of existing and potential control measures. Simulation modelling provides a useful tool to investigate the effects of landscape attributes and host communities on the population dynamics of ticks, assessing the efficacy of eradication and control strategies at different spatial and temporal scales.

Individual-based, spatially explicit simulation modelling has been a useful tool in assessing the effectiveness of CFT eradication strategies (Wang et al. 2017). Despite its recognized limitations, the model presented in this study can be useful in testing the efficacy of control measures under a variety of host community hypotheses, by comparing the temporal response of CFT populations to a variety of WTD habitat preferences and host/eradication scenarios, at the finer habitat-level spatial scales simulated in this study.

7 CONCLUSION

Several challenges exist in the development of multi-host models in disease ecology, all of which have to do with the necessity of an improved understanding of the mechanisms and processes by which vector and pathogen maintenance is influenced by diverse host-agent interactions (Buhnerkempe et al. 2015). The development of a simulation model designed to explore the effect of WTD habitat preferences on the population dynamics of CFT was justified by the uncertainty of the role that behavioral characteristics of ungulate hosts, such as habitat use, play in the effectiveness of control strategies for vectors of diseases.

The usefulness of this model for assessing the effect of WTD habitat preferences on the population dynamics of CFT and the effectiveness of eradication strategies was evaluated following a multi-step approach. This approach involved a) verifying that host habitat preferences and movement rules included in the model generated the expected temporal patterns of host-seeking larvae and adult ticks under a wide range of conditions, b) comparing simulated population-level CFT dynamics to patterns reported in the scientific literature, and c) examining the sensitivity of simulated tick population to changes in host habitat preferences.

Cattle dominated the system, and responses in densities of CFT to changes in WTD habitat preferences were not evident at the landscape level. However, differences in CFT densities at finer spatial scale (i.e., habitat type) indicated that within those habitats least preferred by cattle, temporal trends in CFT populations were influenced by habitat preferences of WTD. My results

suggested that when cattle were present, the role of WTD in maintaining tick populations could be underestimated, due to a disproportionate effect of cattle at the landscape level.

The role of different spatial scales in assessing the effect of WTD on the population dynamics of CFT was evident. The particulars of the interaction tick-habitat preference-landscape were difficult to see at broader spatial scales. However, when the system's response was examined at finer spatial scales, interesting results supporting the idea that WTD habitat preferences play an important role in maintaining CFT populations at the landscape level, through their compounded effect with habitat type, were obtained.

Current and future problems driven by global change require a multi-actor approach to develop effective and sustainable strategies to prevent infestations and establishment of CFT (Pérez de León et al. 2012). Both native and exotic wildlife that co-exist with cattle in South-Texas rangelands may aid in sustaining CFT populations and related tick-borne diseases. Efforts to better understand the tick-host-landscape interaction, including changes in tick distribution, ecology, host utilization, and disease epidemiology, are justified on the grounds of the complicated nature of these interactions.

My model seemed useful in exploring the outcomes of possible eradication strategies, revealing interesting relationships between behavioral characteristics of ungulate hosts and habitat-level suitability for CFT, which likely interact at different spatial scales to influence CFT population trends. The refugia effect in time and space seemed to be driven by the interaction between hosts and habitats. Although potential refugia areas (i.e., mixed-brush) were not the best habitats in terms

of their suitability for tick survival and development, the results of this study indicate that habitat suitability in this system is related not only to climate variables, but also to the potential of CFT to disperse throughout the landscape, mediated by the use of space by WTD.

Pérez de León et al. (2012) highlighted the risks to CFT re-infestations from an increase in species diversity and population densities of free-ranging exotic ungulates, stressing the need for integrated strategies to sustainably eradicate CFT populations in the United States. The results of the present study support the idea that WTD are capable of maintaining CFT in the absence of cattle, suggesting that the use of space by WTD, mediated by their habitat preferences, could play a major role in the distribution of CFT across the landscape, with implications for the maintenance and extent of quarantined areas.

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